

V. *Contributions to the Study of the Bionomics and Reproductive Processes of the Foraminifera.*¹

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¹ This paper, recording the observations of some years past, was written in the months of January and February, 1914, at the instance of my old and valued friend, the late Sir JOHN MURRAY, K.C.B., F.R.S., whose kindly expressed intention, an intention frustrated by his tragic death on March 16 of that year, had been to communicate it to the Royal Society. Throughout the months of January and February, I corresponded with him upon the subject, and the Section VII was submitted to and revised by him in manuscript. From March 4 to March 6, I was with him in Edinburgh, examining his stored material and checking observations recorded in the other sections of the paper. It was then that he placed at my disposal the original laboratory note-books kept by him from day to day on board H.M.S. "Challenger," with free permission to make what use of them I thought desirable. Of that permission I have availed myself in Section VII, with a view to clearing up the hitherto doubtful question as to the "monadiform bodies" recorded by him as occurring in *Cymbalopora bulloides*; and also in Section VIII, in which the vaguely recorded "siliceous Foraminifera" of Dr. BRADY's monograph are explained and, I think, accounted for. The extracts from these note-books constituting Appendices A and B to this paper were submitted to and approved by him a few days before his death. I may, perhaps, be allowed to record in this place a tribute of affectionate esteem for an old friend, coupled with an expression of my sense of a grievous personal loss.

"If we are ever to escape from the obscurities and uncertainties of our art, it must be through the study of those highest laws of our science which are expressed in the simplest terms in the lives of the lowest orders of creation."—Sir J. PAGET, "Lectures on Surgical Pathology," 1849.

I. INTRODUCTORY.

The protozoologist who devotes himself to the study of the Testaceous Sarcodina¹ enters upon a task which is beset with difficulties which are, to a significant degree, insuperable. It is not so much the minuteness of the objects under consideration which is responsible for these difficulties, for, in the present and ever-advancing state of perfection of microscopical apparatus for the facilitation of technique, this is a difficulty which is more or less easily overcome. The mechanical difficulties are presented by the shell, which distinguishes the Foraminifera proper, the external skeleton of the organisms, which, whether they are calcareous, or whether they are arenaceous, that is to say, whether their shells consist of carbonate of lime separated from the surrounding media by some mysterious function of the protoplasm, or whether they are built together of fortuitous or selected materials, cemented together by a substance secreted by the organism, renders the examination of the living animal and the study of its life-history a task to which very definite limits are set. An examination, in the vast majority of species, of the nuclear conditions and changes can only be carried out upon individuals which are dead, and, at best, have been preserved in some recognised fluid (such as Schaudinn's), the precise nature of the effect of which upon the dead protoplasmic body it is impossible accurately to calculate. The geographical difficulty is almost equally great, for many of the largest, and many, if we may use the word, of the "idiosyncratic" forms, are tropical species, having intimate relationships with species inhabiting temperate or even Arctic zones, and it becomes a physical impossibility to examine and compare these organisms alive, regard being had to the fact that to arrive at any satisfactory conclusions the observer must be on the spot to examine the animal when freshly gathered from the littoral zones, or dredged from considerable depths. In the latter case, it is unnecessary to advert to the difficulties inseparable from the work when carried out during the cruise of a surveying ship, however perfectly its laboratories may be equipped, and the best results that the biologist can attain are therefore to be derived from material preserved fresh upon such cruises, or from slides mounted with the haste inseparable from such work when carried out under such conditions.

It is consequently to a great extent only by the observation of carefully sought, or

¹ I make use of the term "Sarcodina," proposed by BÜTSCHLI (B. 1882-9, P.) to define the organisms with which we are concerned, in preference to the term Rhizopoda. It is true, however, that the taxonomic position of these organisms is still, to some extent, in dispute.

of accidentally discovered, resultant effects of the life-activities of these organisms that the student of the Foraminifera is enabled to supplement his observations made upon such members of the group as circumstances enable him to study in the living condition, with a view to arriving at a solution of the intricate problems, for the most part still very obscure, presented by the vital mechanics of such elementary organisms.

When studying the life-history of the Foraminifera, Palæontology gives no assistance. As EARLAND and myself have had occasion elsewhere to observe: "We might reasonably expect that among the earliest geological records would occur Foraminifera of simple and ancestral types, and that subsequent geological periods would show a constant progression in their development. Such, however, is not the case. So far as our geological knowledge carries us at present, the Foraminifera make their first appearance in the rocks at a highly differentiated stage, and among the earliest recognisable groups are many species which are still existing and dominant types to-day."¹ The observations of EHRENBURG and CHAPMAN are conclusive upon this point;² we have no evidence of the existence of any primitive or monothalamous types in the earliest pages of the geological record.³

Though we have advanced a long way beyond the condition of vagueness with regard to these organisms recorded so lately as 1881 by SCHLUMBERGER,⁴ the ultimate clue to the life-history of the Foraminifera is, I think, most probably to be found in the study of the naked or amoeboid forms. There is little doubt that the marine *Proteomyxa* are true Foraminifera,⁵ and RHUMBLER, in his 'Zusammen-

¹ Cf. M. 1912, I.S.P., p. 464. I may call attention in this place to the discovery of the species *Spirillina groomii* by CHAPMAN in the Cambrian rocks of the Malverns (C. 1900, U.C.M., p. 259, Plate 15, figs. 1, 10, 11), and the occurrence of living specimens of the same species (probably the oldest existing specific form of life) recorded by myself and EARLAND, from the West of Ireland (H-A. and E. 1913, F.W.B., p. 4, Plate 1, fig. 1, and 1913, C.I., p. 107, Plate 9, figs. 2, 3); cf. H-A. and E. 1913, F.W.B., p. 2. It behoves one (as Dr. WALLICH has remarked in referring to *Bathybius*) "to speak with bated breath of the mighty dead" (W. 1877, G., p. 163), but a passing reference is permissible to the relatively vast literature which has collected around that controversial organism *Eozoon Canadense*, accepted without question by W. B. CARPENTER, and convincingly rejected by KARL MOEBIUS. The controversy has recently shown signs of Palingenesis.

² E. 1858, S.G.P., p. 234, Plate 1 (Lower Cambrian), and C. 1900, U.C.M., p. 257, Plate 15 (Upper Cambrian). These recorded fossils are referable to at least five genera: Verneuilina, Bolivina, Nodosaria, Pulvinulina, and Rotalia, none of which can be said to be of simple or primitive types.

³ Prof. WALTER HOWCHIN paid particular attention to this feature of our study in his Anniversary Address before the Royal Society of South Australia in 1897 ('Proc. Roy. Soc. S. Aust.,' pp. 107-8 (1897)).

⁴ "On ignore la composition exacte et les fonctions du protoplasma soi-disant élémentaire qui constitue leur corps; on ignore s'il est identique ou différent suivant les genres; on ne sait par quel procédé il s'assimile la nourriture dont il a besoin, par quels moyens il fixe le calcaire ou la silice contenu dans l'eau pour en construire sa coquille. La reproduction de ces organismes est encore un mystère." S. 1881, etc., N.F., No. 1, p. 5.

⁵ See S. J. HICKSON, Article "Proteomyxa" in L. 1909, T.Z., pp. 9, 10; cf. also L. 1903, F., pp. 51, 52.

stellung,¹ has properly included the Amœbæa among the Reticulosa, which he divides into two orders, Nuda and Foraminifera, proceeding from the Nuda to the Foraminifera proper.² It is not unlikely that the study of the life-history of the Foraminifera proper will afford the best results if pursued "along the lines of least resistance"—commencing with the Gromiidae, and thence to the chitinous phases of the Miliolidae, in which condition the investment of the organism (it being confined within a virtually transparent envelope) affords an opportunity for examination with comparatively low-power water-immersion objectives which is not afforded by any of the more robustly covered genera.³

(I may perhaps be allowed to conclude this Introduction by pointing out that this paper records many observations the complete biological significance of which is as yet quite obscure, and adumbrates some theories which have not yet been completely worked out. I have nevertheless recorded these observations at the suggestion of Sir JOHN MURRAY, in the hope that they may prove useful to future investigators in the event of my not being able to complete these studies myself, a task which must involve many years of assiduous work.)

II. THE PROTOPLASMIC BODIES OF THE FORAMINIFERA.

A consideration of the properties of protoplasm in general would lead us very much further than we have any licence to go in this place, but some not insignificant observations upon the properties, and above all upon the "behaviour" of that of the Foraminifera in particular, are inseparable from the task which is before us, namely, a consideration of the observed results of some of its most highly specialised functions. We cannot go into the actual nature of protoplasm and its foam-like and alveolar structure, which have been so ably demonstrated and considered by BÜTSCHLI,⁴ SCHAUDINN,⁵ RHUMBLER, and others, but the point upon which we must

¹ R. 1903, Z.R.F., p. 182.

² It may be convenient in this place to recapitulate the terse definition of "Foraminifera" given by LISTER (L. 1903, F., p. 47):—"Protozoa, the protoplasm of which secretes a test (or shell) and is protruded in fine thread-like pseudopodia, which branch freely and anastomose with one another, and presents no obvious differentiation into ecto-plasm and endo-plasm." To this I would add that:—"The test may be chitinous, calcareous, arenaceous, or spicular (*Carterina*) and the organism may be mono-nucleate or multi-nucleate."

³ SCHAUDINN, in his observations upon *Patellina corrugata*, tells us (S. 1895, P.F., p. 182) that he made the organisms reveal their nuclear conditions *through* the shell in the living state by causing them to observe a strict régime, the cytoplasm being opaque when the creatures had access to animal food, but transparent when restricted to a rigidly vegetarian diet.

⁴ O. BÜTSCHLI, 'Untersuchungen über Mikroskopische Schäume und das Protoplasma,' Leipzig, 1892; translation by E. A. MINCHIN; 'Investigations on Microscopic Foams and Protoplasm,' London, 1894.

⁵ F. SCHAUDINN, "Krankheitserregende Protozoen. II.—Plasmodium vivax," 'Arb. a. d. K. Gesundheitsamte,' vol. 18, p. 188 (1902) (Collected Works, Hamburg, 1911, p. 390, Plates 21-23).

primarily fasten our attention is its essential fluidity, as demonstrated by the streaming movements which are to be observed in the pseudopodia of the Foraminifera, and its general behaviour when extruded from the shell, and we must ask ourselves whether we can reconcile with such essential fluidity any "behaviour" which would appear to depend upon structural features, or upon any kind of co-ordination. MAX SIGMUND SCHULTZE declared against such a possibility with no uncertain voice in 1854,¹ but CLAPARÈDE and LACHMANN, writing in 1858, entreated the scientific world to suspend its judgment until the protoplasm of the Rhizopoda should find the reagent which would unveil its mystery, as chromic acid had resolved the microscopic anatomy of the central nervous system.² In the present state of our knowledge it is extremely doubtful whether the protoplasm of the Foraminifera is divided, as in the majority of the Protozoa, into endoplasm and ectoplasm, but if it be so, we may assume that, in common with the other Protozoa, the endoplasm being specially concerned with the internal affairs of the organism, the ectoplasm "is the seat of those functions which are connected with the relation of the organism to the outer world and of the environment in which it lives."³ It is more convenient, therefore, to describe the protoplasmic body of the Foraminifera as Nucleus and Cytoplasm, unless we adopt RAY LANKESTER's term "periplasm" for the latter.⁴

The first and self-evident function of the protoplasm of the Foraminifera is that of locomotion, the second, which is obscure so far as the actual process is observable, is that of the capture and digestion of food materials upon which the organism lives. Both of these functions have been carefully observed and elaborately described. One of the most striking objects which presents itself to the student of the living forms is the dignified method of progression (by turns and twists of the body attached by the pseudopodia streaming from its aperture) exhibited by a living Miliolid on the glass side of a tank, or by any member of the *Gromia* family studied in captivity.

¹ "Die Bewegungen dieser Wesen erscheinen willkürliche, doch sind bestimmte Organe der Bewegung und Empfindung in diesen einfachen Thierleibern noch nicht differenziert. Sie können nicht vorhanden sein in einem Körper, dessen Theile so durchaus gleichwerthig sind, dass jedes Körnchen desselben in jedem Augenblick die Stelle mit einem jeden anderen vertauschen kann." (S. 1854, O.P., pp. 7-8.)

² "Cette coquille à structure si incroyablement compliquée serait secrétée par une masse de gelée informe et à peine organisée? C'est, ce nous semble, une absurdité. L'animal qui secrète le test calcaire d'une *Polystomella* . . . ne peut être une masse de sarcode. L'existence même de ces tests si compliqués nous enseigne que, lorsque nous ne savons rien reconnaître en fait d'organisation dans les parties molles de l'animal, nous ne devons en accuser que notre méthode et nos moyens d'observation. Où en serait l'anatomie microscopique du système nerveux central sans l'acide chromique et les autres agents analogues? Le sarcode des Rhizopodes n'a pas encore trouvé son acide chromique." And again—"Il est bien difficile à la raison humaine de se représenter des animaux vivants et doués de fonctions physiologiques variées, tout en restant confinés dans un degré d'organisation qu'on ose à peine taxer d'organisation véritable." (C. and L., 1858, E.I.R., pp. 414 and 422.)

³ M. 1912, I.S.P., p. 44.

⁴ L. 1909, T.Z., p. xxi.

A remarkably fine and active *Gromia*, one of a series which I have been for some time observing in captivity (with special regard to the symbiotic algæ which are present in these organisms in large quantities and in a high state of development)¹ (figs. 1 and 2), crawled from the mud layer of the tank up the stems of the algæ shown in the figure (fig. 3), a distance of 2 cm., and then stepped off, as it were, on to the glass against which the alga was growing and came to rest about a centimetre above it (fig. 4), in a little under three hours.²

I am not aware that this process of "stepping off" has been previously observed or recorded. The summits of the stems (fig. 3) were at their nearest 3 mm. from the glass of the tank and the *Gromia* made its ascent up the further stems. The pseudopodia were fully extruded and anastomosing freely on the glass and in the water, where they appeared and disappeared in and out of focus. Arrived at the top of the stems, the pseudopodia perceptibly thickened, and the organism "took off" and drew itself on to the glass in one rapid contraction of the pseudopodia, carrying with it the remains of its bunch of protoplasm, and mud and symbiotic algæ. It then proceeded upon its upward course.

The function of the pseudopodia as an apparatus for capturing food particles has been made familiar to every student of the group by the frequently, I might almost say, everlastingly, reproduced figure of *Gromia oviformis* which we owe to MAX SCHULTZE.³ It is a common occurrence when Miliolinæ of the larger-mouthed species are mounted in balsam and viewed by transmitted light, to see very clearly the Foraminifera and Diatoms which have been captured as food for the organism at the moment when it became a martyr to science. In figs. 5 and 6 are two specimens of *Miliolina durrandii*, Millett, one (fig. 5) containing a recently ingested microscopic *Massilina secans* (d'Orb.), the other (fig. 6) a very much smaller specimen, which is

¹ To the life-history and behaviour of this species, and to its relations with its symbiotic algæ, I hope to devote a memoir in the near future. The specimens, which can be gathered in great quantities in the neighbourhood of my laboratory at Selsey Bill (Sussex), fall into the three groups of *Gromia dujardinii*, Schultze, *Gromia oviformis*, Dujardin, and *Gromia brunnerii*, Blanc, and present a very prolific field for research, the chitinous envelope of the creatures being particularly pellucid, and showing relatively large masses of symbiotic algæ of a peculiarly vivid green colour embedded in a rich orange granular cytoplasm. These algæ are extruded in considerable quantity from the aperture, when the animal is in a state of activity, mingled with mud and other rejectamenta of the organism, as shown in the figures. It will be observed that as the animal has crawled up the living stem of the algæ, much of this *débris* has been, as it were, combed away, and left among the stems, leaving a small mass of practically clean protoplasm studded with green symbiotic algæ extruded from its aperture, when it moved from the alga on to the glass side of the tank. These Gromids, being very robust, hardy, and active, afford opportunities for the study of many interesting phenomena which I propose to discuss on a later occasion.

² SCHLUMBERGER measured the pace of an active *Peneroplis* which covered 0.18 cm. in three minutes, giving a distance of 3.6 cm. in an hour. (S. 1881, &c., N.F. 1882, No. 3, p. 41.) JEFFREYS, on the other hand, limits the 24-hour journey of a Miliolid to 0.25 inch, but this was not an observation of continued progression. (J. 1855, N.B.F., p. 210.)

³ S. 1854, O.P., Plate 1, fig. 1.

making a meal off one specimen of each of the Diatoms *Biddulphia pulchella* and *Surirella striatula*.¹

It is a not uninteresting question to ask whether this ingesting action of the pseudopodia is wholly voluntary or partially, at least, a physical reaction dependent upon the surface-tension relations existing between the protoplasm and the body ingested (*cf.* RHUMBLER, *post*). Whether the object caught in the pseudopodia be a nutrient and useful one or not, the first phenomenon which attracts the attention of the observer is a streaming of the protoplasm to the point of contact and an active anastomosis of the threads of the reticulum at that point, the object being then carried to the aperture of the shell and engulfed. There can be no doubt as to the utility of the process, in the case of the Miliolids figured in figs. 5 and 6, but fig. 7 opens up the question whether the action is not primarily reactionary, and ultimately dependent on the chemical nature of the two substances involved in the reaction, bringing about a result comparable with the effect of peristalsis, though I do not for a moment suggest that a fluid and undifferentiated mass of protoplasm can be conceived to exhibit peristaltic action.² Whilst watching the evolutions of a specimen of *Massilina secans* in a drop of sea-water on a slide, a dust particle, presumably a hair (or perhaps a filament of wool or jute from the observer's coat sleeve or elsewhere), fell upon the extended pseudopodia and was immediately seized and enveloped by them. It was then carried to the aperture of the shell, and in the course of half-an-hour was engulfed endways. The living Miliolid was then picked up and rapidly mounted as a transparent object in glycerine (fig. 7). It will be seen that the hair has reached the termination of the ultimate chamber, has turned round twice, and the ingestion of the latter end of the hair has forced the end which first entered almost as far back as the aperture of the shell. With this may be compared the absorption by *Amœba verrucosa* of filamentous algæ which are imported into the interior of the body and there coiled up and digested, and RHUMBLER's observation on a similar action exercised by a drop of chloroform in water upon a thread of shellac.³ Fig. 8 represents the decalcified protoplasmic body of another specimen which had been induced to repeat the process. In this instance, though the protoplasmic body has suffered in mounting, it can be made out that the hair (?) has passed beyond the ultimate chamber into the penultimate chamber.

That protoplasm is endowed with a certain measure of sensory function is a well

¹ With regard to the digestive functions of the Rhizopodal protoplasm, see C. 1901, P., pp. 52 and 91. I have recently found a very perfect specimen of the very minute species *Cassidulina bradyi* var. *elongata*, Sidebottom, as a result of accidentally crushing a shell of *Cymbalopora bulloides*, d'Orb.

² Many authors have called attention to the peristaltic waves of contraction in some of the more elementary protozoa. *Cf.* CALKINS, 1901, P., p. 43.

³ M. 1912, I.S.P., p. 50, fig. 23, L. RHUMBLER, "Physikalische Analyse von Lebenserscheinungen der Zelle," 'Archiv für Entwicklungsmechanik,' vol. 7, p. 103 (1898).

recognised fact.¹ The living Foraminifer is apparently sensitive to light.² I had occasion to prove this, by taking advantage of the fact, in photographing the Gromiidae to which reference has been made, of which a specimen appears in figs. 9 and 10. In that case, the Gromia having become lost among weeds, a small hole was punched in a piece of black paper and affixed to the glass side of the tank, and a beam of strong light directed through it; within an hour three independent specimens of Gromia had crawled into the circle of light thus formed.³ That they are sensitive to touch is made manifest to anyone who observes the living animal, for if the extended pseudopodia are disturbed with a needle beyond a reasonable point the animal sulks, retracts its pseudopodia, and in my experience may remain sulking for days.⁴ A much more delicate and controversial question is that of the function of the protoplasm, when extruded in the form of pseudopodia, as a weapon of offence or defence. It is an interesting question whether the pseudopodia do, or do not, secrete some toxic, as well as sticky, substance which not only catches but kills entangled organisms, such as is seen in the well-known figure of SCHULTZE above referred to, which has been cited as a proof that digestion of food-victims may take place outside the shell in the network of protoplasm formed by the anastomosing pseudopodia,⁵ but it will be observed in SCHULTZE's figure that several Pleurosigmata equal in size to the entangled individual are indicated inside the body of the animal.⁶ Nothing in the nature of the trichocysts found in many of the Infusoria⁷ has been observed in the Foraminifera, but in the small observation-tanks, on the glass sides of which I have followed the behaviour of living Foraminifera by means of the Zeiss-Greenough tank microscope, it has been a matter of almost momentary occurrence to see a tiny Copepod blunder against the fully extended pseudopodia of a robust Miliolid, and instantaneously fall to the bottom of the tank apparently dead. The Copepod is, however, only stunned, or by some unidentified means terrified, for at the end of, at the most, two minutes, it seems to stretch itself and dart off once more upon its apparently gay and

¹ M. 1912, I.S.P., p. 61.

² CLAPARÈDE and LACHMANN in 1858 established the fact that *Lieberkuehnia Wagoneri* was affected by a transition from darkness into light (C. and L. 1858, E.I.R., p. 465).

³ At the same time I do not lose sight of the possibility that, the spot of light having attracted swarms of monads (as it always does), perhaps the Gromia crawled into the circle in pursuit of them.

⁴ Regard being had to the insistence in this paper upon the highly functional "behaviour" of Foraminiferal protoplasm, it is perhaps desirable at once to point to the fact that no suggestion of any specialised sensory constituent is here put forward. In unicellular organisms there is little room for doubt that all parts of the protoplasm are sensitive to stimuli, without development of any sensory constituent. (Cf. D. 1912, E.B., p. 188.)

⁵ C. 1901, P., p. 91.

⁶ This latter feature is generally exaggerated in the reproductions (Cf. M. 1912, I.S.P., fig. 21). The paralysing effect of the pseudopodia of the Heliozoa upon Infusoria has frequently been observed. (Cf. WELDON and HICKSON, "The Heliozoa," in L. 1909, T.Z., p. 17.)

⁷ Cf. M. 1912, I.S.P., pp. 46 and 447, and C. 1901, P., p. 50.

irresponsible career.¹ Of extraordinary interest in this connection are the observations upon the distinctions and differences shown by their "behaviour" to exist between the protoplasmic bodies of Sarcodina (Foraminifera) of the same species and genus made by JENSEN.² He established by observations made upon Orbitolites and Amphistegina that the pseudopodia of two independent individuals do not blend at contact, but on the contrary appear to repel one another—in marked contrast to the free anastomosis of the pseudopodia of a single individual. He concludes from this that the protoplasm of different individuals is physiologically different—apparently in its chemical composition. SCHAUDINN elaborated these observations with the result that he found that JENSEN's observation was confirmed in the case of individuals whose nuclei showed differences (*e.g.* mono-nuclear and multi-nuclear individuals, and in cases in which one nucleus was in process of chromidial fragmentation, and the other "at rest"), but he found that as between individuals whose nuclei were in a state of rest in the primordial chamber, the pseudopodia showed no antipathy to what may be called hetero-anastomosis. These phenomena, though not of my own observation, I quote as an illustration of one of the marked differential and potential capacities of the Foraminiferal protoplasm.

Of what I may perhaps be allowed to call the higher and, if I dare say so, psychological functions of the Foraminiferal protoplasm extruded as pseudopodia I shall have to speak later.

III. THE PHENOMENON OF SO-CALLED "PLASTOGAMIC" OR "ASSOCIATED" TESTS.

The reproductive processes of the Foraminifera that have engaged the attention of biologists may be broadly divided into reproduction by (i) amœbulæ, (ii) flagellisporos, and (iii) the phenomenon which protozoologists have agreed to designate by the term "plastogamy" or "plasmogamy."

With regard to the phenomena of amœbula production, and the syngamy of flagellisporos, the recorded observations of SCHAUDINN, of LISTER, and of WINTER recapitulate and constitute all that is at present known upon the subject, whilst as regards "plastogamy," rightly or wrongly, I am of opinion that an improper significance has been given to this phenomenon of "association" of individuals,—a term which, for reasons which are becoming obvious, and which I hope to render more so, is a more correct definitive term than plastogamy, at all events when speaking of the Foraminifera.

The existing records of observed reproduction by "association" rest upon the observations of SCHAUDINN, who has observed and minutely described the "association"

¹ This paralysing effect was also observed by M. SCHULTZE, exercised by *Gromia* and *Polystomella* upon Infusoria. (L. 1903, F., p. 51.)

² J. 1895, P.U.Z., p. 172.

of pairs,¹ and of greater numbers of individuals, of the species *Patellina corrugata* and *Discorbina globularis*;² a similar association of several individuals has been observed (and recorded) by many writers on the Foraminifera, and particularly by EARLAND in the species *Discorbina parisiensis* among the littoral Foraminifera of Bognor³ and by EARLAND and myself jointly, in this genus and others, in the material dredged from moderate depths in the Kerimba Archipelago by Dr. J. J. SIMPSON⁴ (fig. 11).

I may say at once that, for reasons that will presently appear, I do not regard this "association" of pairs of individuals as a sexual union of two individuals, and I do not consider that the association of several individuals as observed by SCHAUDINN in *Patellina corrugata*, and by EARLAND and myself in Discorbinæ of various species, to be either sexual, or to have any relation to the frequently observed association of single pairs, which, as will be seen, I consider to afford evidence of an entirely different reproductive process. EARLAND, in his paper on the Bognor Foraminifera, records three facts which in my opinion support this contention; (1) that the apertures do not necessarily coincide, and that in a great number of instances the edges overlap, or one specimen is set to one side of the vertical axis of the other specimen; (2) that sometimes three, four or more specimens are united in the same more or less asymmetrical manner; (3) that in many instances the "associated" specimens represent varying types. In SCHAUDINN's well known figure (*loc. cit.*, p. 185) the plastogamic pair are set in a similarly eccentric manner to one another, and he points out that the formation of the young shells from amoebulæ takes place from the cytoplasm of the parent shells after it has been extruded into the deep cavity (or *Nabelhöhle*) formed by the more or less exact coincidence of the deep umbilical depressions which are characteristic of *Patellina corrugata*. Now, regard being had to the observations of LISTER already referred to,⁵ it seems to me, if not clearly demonstrated, at least very probable that in such cases as this, the amoebulæ have

¹ In drafting this paper I hesitated long whether or not to make use of the word "association" instead of the word "duplication." Though the latter term is not satisfactory, it might be, for some reasons, preferable for the purpose that I have in view, regard being had to the significance attached to the former expression. I am indebted to Prof. MINCHIN for the following note:—"The strict definition of the term 'association' is an approximation or union, or even fusion, of two individuals about to form gametes in close proximity, as in Gregarines, where the term was first used. 'Association' has a sexual significance in reference to preparations or preliminaries for a sexual act to be performed, *not by the associated individuals themselves*, but by the gametes produced by them." In what follows it will be made clear that I use the term "association" without any sexual significance whatever.

² S. 1895, P.F., pp. 181 *et seq.* From a close study of SCHAUDINN's work it would appear that the actual processes of reproduction observed by him were confined to *Patellina corrugata*, and he seems to have argued by analogy in the case of *Discorbina globularis* after observation of the "associated" pairs to which reference is about to be made.

³ E. 1905, F.B.S., p. 221.

⁴ Our monograph upon the Foraminifera of this area is now in course of publication: Part I in 'Trans. Zool. Soc.,' London, vol. 20, pp. 363-390 (1914); Part II, 1915, in the press.

⁵ L. 1903, F., 62-70; and L. 1895, L.H.F.

been formed from the emerged protoplasm (as observed by him in *Polystomella crispa*) of a number of shells which have fortuitously come together. SCHAUDINN states that he was able to observe that no fusion of the nuclei of these "associated" individuals took place. For the reasons given above, and to be set forth later, I do not consider this "association" to be in any way sexual, and therefore this particular method of reproduction, *i.e.* the theory of "Plastogamy," does not concern us any further for the purposes of this paper.

What, however, does concern us at present, and the only points in connection with the reproduction of the Foraminifera to which I propose to address myself in this paper, are (1) the production of viviparous young more or less fully developed, and already invested with a calcareous test to the extent of two or more fully developed chambers (in the case of the polythalamous genera), and of perfect but infinitely minute individuals (in the case of the monothalamous genera), and (2) the real significance of the phenomenon of the apparent "association" between two individuals which has hitherto been described as plastogamy,¹ and which I am describing as "association." One observation alone is common to both enquiries, and that is, that so far as protracted research has enabled me to judge, no sign of viviparous young inside the parent shells has ever been observed in associated pairs, by the process either of careful sectioning, or of mounting in transparent media.² From this point the two enquiries entirely diverge.

IV. VIVIPAROUS GENERATION.

It is necessary to state at once that I do not propose to consider in this connection the recorded observations of the presence of embryonic shells or "primordial cells," that have been seen by transmitted light in the terminal chambers of several species. Of this nature are the "Kugeln" described in *Rotalia* by SCHULTZE,³ in *Cristellaria* by BRADY,⁴ and to a remarkable degree in *Peneroplis* by SCHACKO,⁵ which were doubtless amœbulæ formed within the parent shell, similar in their naked condition to those figured by LISTER (*passim*) swarming out of *Polystomella*. By viviparous generation I wish to imply only the development *within the parent*

¹ Plastogamy may be described as a union of two individuals, entirely independent of syngamy, since the cytoplasm only of the individuals is fused, without any fusion of the nuclei. The term seems to have been first employed by Prof. HARTOG in this sense. (H. 1892, P.R., p. 7.)

² Since this paper was written we have been led by the discovery of a new type of Foraminifera, of which we could not spare a specimen to sectionise, to have skiagraphs made of several densely calcareous and arenaceous species. These have been made for us by Mr. J. E. Barnard, and were recently exhibited before the Zoological Society ('J. R. Micr. Soc.,' 1915, p. 1; and 'Proceedings,' p. 87; see also 'Proc. Zool. Soc. Lond.,' 1915, p. 152. This process, which is quite conclusive, has also failed to reveal any sign of young shells in process of formation in "associated" pairs of shells.

³ S. 1854, O.P., p. 27.

⁴ B. 1884, F.C., p. 543, Plate 68, figs. 1-2.

⁵ S. 1883, U.F., p. 443, Plate 12, figs. 1-3.

shell of fully formed polythalamous young, already endowed with a calcareous investment.¹

It will therefore be well to present at once illustrations of the ultimate phenomena observed in this connexion.² Fig. 12 represents a remarkable specimen of *Discorbina mediterraneensis* which I found attached to growing *Corallina officinalis* in the rock-pools on Clare Island Strand (Co. Mayo) and have already figured in our Clare Island monograph.³ This specimen was split by myself from the Coralline to which it was attached and *had not been in a condition of so-called "plastogamy."* This is shown by the ragged and broken edges of the base of the shell. Fig. 13 represents a specimen of *Discorbina wrightii* and fig. 14 of *Discorbina parisiensis* which are seen to be filled with broods of uniformly developed microscopic young. In these cases part of the base of the shell has been neatly dissolved away by the solvent action of the protoplasm (to which I propose to address myself later when dealing with *Cymbalopora*) preparatory to the liberation of the young. The specimens were found in the condition in which they are figured, and I do not think it is over-venturesome to suggest that, if these represented separated individuals of "associated" pairs, the others of which had been broken away, the aperture would not have been thus neatly rounded, whilst on the other hand, if an associated individual had been dissolved from off the other by the solvent action of the protoplasm, it is reasonable to suppose that the cavity would have extended to the outer edges of the shell as in the case of the split-off specimen from Clare Island.⁴

¹ In the year 1882 the late OLRÉY TERQUEM stated, in a note on p. 10 of his "Foraminifères de l'Eocène des Environs de Paris" ('Mem. Soc. Géol. France,' S. 3, vol. 2, Mem. 3), after putting forward the theory that the Foraminifera may reproduce themselves by budding (a theory which I am addressing myself to the task of proving in this paper), "M. SCHLUMBERGER possède une Quinqueloculine entièrement transparente dont la dernière loge est remplie de Quinqueloculines embryonnaires: les Foraminifères seraient donc des animaux ovo-vivipares à l'instar de certains Gastéropodes (*Paludina vivipara*)."

(See following note.) It was, however, EHRENBURG in 1841 who first observed these primordial young in a *Spirillina* to which he consequently gave the specific name *vivipara* ('Abh. k. Ak. Wiss. Berlin,' p. 422, Plate 7, fig. 41 (1841)), and in 1878 A. SCHNEIDER in his "Beiträge zur Kenntniss der Protozoen" ('Zeitschr. f. Wiss. Zool.,' vol. 30, Sup., p. 446) had published the results of his researches regarding the reproductive processes of the genus *Miliolina*, observations which have since been fully confirmed, and which had been to a great extent anticipated by MAX SCHULTZE. (See MÜLLER'S 'Archiv,' 1856, p. 165, and 'Q. Journ. Micr. Sci.,' vol. 5, p. 220 (1857).)

² It may not be without interest if I call the student's attention to the figure (Plate 3, fig. 11) of TERQUEM'S "Essai sur le Classement des Animaux qui vivent sur la Plage . . . de Dunkerque" (Paris, 1875, etc.). This is undoubtedly the first figure ever given of viviparous young contained within the mother-shell—but TERQUEM did not recognise the phenomenon. He described the shell (p. 30) as "aplatie en dessous et formée d'un anneau externe, excavée dans le milieu et munie de six sphères élevées." On this account he named his species, as a new one, *Rotalina ovigera*, but his "elevated spheres" are undoubtedly viviparous young, and his species is probably *Discorbina parisiensis*.

³ H.-A. and E. 1913, C.I., pp. 119, 120, Plate 10, fig. 1. This figure was in many respects unsatisfactory, and I take this opportunity of figuring the specimen again.

⁴ SCHAUDINN suggests that the growth of the polythalamous young in *Discorbina*, *Planorbulina*,

Fig. 15 represents a most remarkable case of viviparous reproduction in a large specimen of *Planorbulina mediterraneensis* gathered by myself in the Bay of Brégançon, near Hyères (Var), on the shores of the Mediterranean Sea. It will be readily admitted that an outspread and almost invariably adherent form such as this cannot by any stretch of imagination be assumed to have detached itself in company with another specimen, and that the two individuals should then have reared themselves up on edge so as to fasten their basal planes to one another, and then to have dissolved themselves apart, leaving one in the condition in which it is seen in the figure. If this had been the case it is not unreasonable to suppose either that the whole of the basal plate would have been shorn off, or dissolved away, whereas it is quite obvious that the chambers containing the young (where they are exposed) show unmistakable signs of having been split off from the surface to which the creature had been attached, in the process of its detachment. Again, figs. 16–19 represent a remarkably fine specimen of *Orbitolites complanata* picked by EARLAND from the Kerimba Archipelago material, the edge of which has been dissected away so as to show the contained brood of young *in situ*: fig. 17 a piece of the shell removed by him for the purpose: and fig. 18 some of the embryonic young, already consisting of the primordial chamber, and the commencement of the first annular series of chamberlets, picked out of the parent shell. Fig. 20 represents a section of a similar shell mounted in balsam. The appearances clearly suggest that the young brood effects its “escape,” as LISTER has observed,¹ “by the breaking down of the outer walls of the brood chambers under the dissolving action of the protoplasm of the young.” This phenomenon had already been observed by BRADY in specimens of *Orbitolites complanata* var. *laciniata* (= var. *plicata* Dana), from the reef off Suva in Fiji,² repeating the observations made by the late W. K. PARKER in the ‘Introduction,’³ and by CARPENTER⁴ in his report on the genus *Orbitolites*. BRADY was of opinion that the var. *laciniata* represented a breeding stage of *Orbitolites complanata*,⁵ but our specimens show no sign of this variation, being of the common tropical plane type, with a smooth periphery. I have no intention of touching even remotely upon the phenomenon of dimorphism

Truncatulina and other genera breaks open the parent shell, an opinion to which I, at one time, inclined myself, but the evidence of the empty shells (*vide post*) seems to point rather to this solvent action and resorption of the parent-shell, by the parental protoplasm, both as regards its internal septa and its base (*cf.* S. 1895, P.F., p. 189).

¹ L. 1903, F., p. 73.

² B. 1888, R.C.O., p. 693.

³ C.P. and J., 1862, I.F., p. 38, Plate 4, fig. 22.

⁴ C. 1856, M.O., p. 212, Plate 4, fig. 11.

⁵ The dimorphism of the Foraminifera had not been studied at the date at which BRADY wrote, to the extent that it has been to-day, and he was far from appreciating the biological significance of the phenomena which he observed and recorded.

in the Foraminifera which has been so ably treated by LISTER,¹ SCHAUDINN,² and others since the phenomenon was first recognised by VON HANTKEN, and elucidated by MUNIER-CHALMAS³ and DE LA HARPE,⁴ but it may be remarked that the specimens in which we have observed this phenomenon have been invariably microspheric. LISTER, however, records that he has observed it in individuals from material gathered off Celebes by Prof. S. J. HICKSON, which individuals were megalospheric, which affords an instance of the irregular life-cycle so clearly tabulated by MINCHIN,⁵ illustrating the highly inconstant method of alternation between sexual and non-sexual generations in the Protozoa.⁶

Finally, it may be observed that SCHAUDINN states authoritatively that, in these associated animals, "the nuclear division and embryo formation takes place mutually in both individuals,"⁷ but, for reasons given above and others to be later adduced, I am of opinion that he took this for granted, and was carried further than he intended in following out a hypothetical sequence of events.

The observed instances of viviparity in the monothalamous Foraminifera are extremely rare. As far as my researches extend it has only been recorded in connection with a single species, namely, *Lagena ornata* (Williamson). The late Dr. CHASTER figured a specimen⁸ containing a quite embryonic shell. We have recently found a specimen (from Scapa Flow, Orkney, fig. 21) containing a fully formed young individual. In this juvenile the typical aperture and entosolenian tube are already fully developed, and the young shell is ready to be set free. This is clearly a phenomenon having no relation to that of associated pairs upon which I have established my theory of the "budding" of Foraminifera, and represents perfect viviparity. It is clear in this instance also that the young shell cannot get free without dissolving away and presumably destroying the parent shell.⁹

¹ L. 1903, F., p. 56, and L. 1895, L.H.F.

² S. 1895, D.F., p. 87.

³ MUNIER-CHALMAS, "Etudes sur les *Nummulites lævigata*, etc.," 'Bull. Soc. Géol. France,' Ser. 3, vol. 8, p. 300 (1880). His theory that the microsphere was brought about by a transmutation of the megalosphere into small chamberlets appears to have influenced BRADY in his views upon the significance of his viviparous Orbitolites (B. 1888, R.C.O., pp. 696-7). The theory was clearly controverted by DE LA HARPE. (See following note.)

⁴ PHILIPPE DE LA HARPE may be said to be the father of research as regards the dimorphism of the Nummulites, which he dealt with in a long series of papers ranging in date from 1874 to 1883. See especially his "Etude des Nummulites de la Suisse," 'Mem. Soc. Paléont. Suisse,' vol. 7, p. 105 (1881), and his letter "Sur l'Importance de la Loge Centrale chez les Nummulites," 'Bull. Soc. Géol. France,' Ser. 3, vol. 9, pp. 171-176 (1881), with the comments (p. 178) of MUNIER-CHALMAS thereupon.

⁵ M. 1912, I.S.P., p. 235.

⁶ L. 1895, L.H.F., pp. 435 and 444.

⁷ S. 1895, P.F., p. 189.

⁸ C. 1892, F.S., p. 62, Plate 1, fig. 6.

⁹ The discovery, since the above was written, of a Miliolina which, on being broken open, revealed

I cannot help being led irresistibly to the conclusion that, in the more familiar cases, we are confronted with the phenomenon of endogenous "budding": that is to say, budding from the nucleus of the parent, by chromidia alone, or together with the nucleus. As MINCHIN has observed, such buds may arise on the surface of the parent body or they may be cut off in the interior of the cytoplasm of the parent, and may remain for some time inside its body, as has been observed in the schizogony of the Neosporidia, and in Arcella, and in some Sarcodina, where it is combined with the formation of secondary nuclei from chromidia.¹ SCHAUDINN records that he has observed in the arenaceous form *Ammodiscus gordialis* (Parker and Jones) the collection and ingestion of sandy particles by the protoplasm of the mother shell, with which it invests the amœbulæ before they depart from it by way of the aperture to lead a separate existence.² I have never observed anything suggesting this, but in the Kerimba Archipelago material we have frequently found primordial chambers (the "Adelosina" stage) of *Miliolina agglutinans* (d'Orb.) already encrusted with relatively large sand grains (fig. 22).

It is not unlikely that in many cases the organism goes into a period of rest³ preparatory to this stage in its life-history supervening, and I think it is not unreasonable to suppose that this accounts for the many instances in which we find Foraminifera, especially of the Rotaline types, not merely growing adherent to algæ and to molluscan and other fragments (for a vast number of species are both adherent and free in their habit of life), but firmly fastened to the surface of alga roots and to calcareous algæ and to mineral fragments by a cement which is indistinguishable, very often, in its composition, from the fine sandy cement which binds together the materials out of which many of the coarsely arenaceous forms build their tests. The most highly developed examples of this method of adherence or "encystment" are to be found in the species *Valvulina fusca* (Williamson) and *Valvulina conica* (Parker and Jones),⁴ and clear traces of it are to be seen at the base of the shell represented in fig. 12.

a fully formed adult second individual inside it, suggests that in these cases some form of "arrested twinning" has taken place (April, 1915).

¹ M. 1912, I.S.P., p. 124. The process which I am postulating has been set forth very lucidly by CALKINS (C. 1901, p. 95) and appears to be entirely confirmed by SCHAUDINN's later observations upon the amœbula-reproduction stage of *Polystomella crispa*. "At the end of the growing stage the whole of the plasma is closely filled with chromidia, whilst the nucleus proper entirely degenerates and falls to pieces." (S. 1903, F.R., p. 548.) SCHAUDINN records the formation, after this, of small nuclei, each of which surrounds itself with an investment of dense protoplasm.

² S. 1894, F.F., p. 162.

³ I was at one time tempted to make use in this place of the phrase "encysts itself," but the term is open to objection and is unsatisfactory. "Encystment" as it is understood among the fresh-water forms appears to be entirely absent in the marine Sarcodina (C. 1901, P., p. 90), but what follows will, I think, make my meaning and reservations clear.

⁴ See B. 1884, F.C., Plate 49, figs. 14-15.

SCHAUDINN affirms that the shells of associated (*copulierte*) Foraminifera are "frequently tightly stuck together with secondary shell substance"¹ (*Kalkmasse*). This I am not in a position to deny, but among the hundreds of pairs that I have examined I have never seen this, though the protoplasm which exudes between the bases of the associated pairs in the performance of its normal functions is, in the later stages of this process, frequently masked with mud, diatom-frustules, and sand-grains—as, indeed, is shown in SCHAUDINN's figure of the associated Patellinæ.²

I wish to make it quite clear that I do not wholly deny the "association" of pairs of individuals, and the fusion of the cytoplasm without any fusion of nuclei, among the Protozoa, which has been described as plastogamy. It exists, for instance, without doubt in the Mycetozoa and the Lobosa,³ but what I wish to lay stress upon is that there does not appear to me to be any evidence that any such "association," whether leading to the formation of viviparous young within the parent shell or no, has been observed among the Foraminifera. Furthermore, I do not think it is necessary, for reasons which I have above set forth, to assume that when the young have been produced their egress is effected by the breaking apart of associated pairs, the evidence appearing to me to point to a dissolution or resorption of the shell wall of the base, to form the necessary opening as in the figures I have given.

And this leads us, in passing, to a consideration of the empty shells, *i.e.* shells which we find in the condition shown in figs. 23 and 24, where, the young having escaped, the whole of the internal septa of the shell have disappeared, a condition which has been observed (though never carried to so complete an extent) in *Bulimina elegantissima* (*vide post*). As LISTER has justly observed, in the case of the microspheric forms (whether the amœbulæ develop inside or outside the parent shell), the whole of the protoplasm of the parent is used up in their production.⁴ These empty shells always present the appearance of a neatly rounded-off margin, which seems to me, as I have pointed out above, to militate against the "breaking out" theory of SCHAUDINN. (See note 4 on p. 238.)

That absorption of the septa does not always, if ever, take place is proved by the discovery of very perfect and beautiful glauconite casts of the protoplasmic bodies of associated pairs, two of which are represented in figs. 25 and 26, from which the calcareous investment and septa have entirely disappeared, showing the whole of the contents of the chamberlets.

¹ S. 1895, P.F., p. 189.

² S. 1895, P.F., woodcut, p. 185.

³ A very interesting and significant account of the plastogamy of *Centropyxis* and *Diffugia* is given by HICKSON in his article on the Lobosa in L. 1909, T.Z., p. 88; *cf.* also CALKINS, who gives many authorities. (C. 1901, P., pp. 96-7.)

⁴ L. 1903, F., p. 72.

V. REPRODUCTION BY FLAGELLISPORES.

The evidence that has been put forward in support of the reproduction of the Foraminifera by the anisogamous conjugation of flagellisporae (as contrasted with amœbulæ) from different individuals, on the part of SCHAUDINN, LISTER and others, marks a very important stage in the study and comprehension of the Foraminiferal life-cycle. It is of comparatively recent date. LISTER was the first to observe and to record with his customary caution the occurrence of flagellate swarmspores in *Polystomella crispa*,¹ though SCHAUDINN had assumed their existence as the outcome of certain observations which I cannot regard as being conclusive.² In 1901 CALKINS pointed out that there was no evidence of their conjugation³ and in 1903 LISTER reiterated this warning.⁴ It was probably immediately after this was written that SCHAUDINN's observations, made contemporaneously, were published,⁵ in which he confirmed and amplified LISTER's observations upon the reproduction of *Polystomella crispa* by amœbulæ, and unhesitatingly supported his records of the phenomena attendant upon dimorphism as exhibited by this species. In this paper he stated that the gametes of *Polystomella crispa* would only copulate when a couple came together, in which each gamete was of distinct parentage, though, regard being had to the extreme minuteness and enormous number of the flagellisporae and the circumstances under which they are discharged and come together, it appears to me that an

¹ L. 1895, L.H.F., pp. 426, 427.

² SCHAUDINN (S. 1895, D.F., p. 92) originally was convinced of the production of the microspheric generation in *Polystomella* by flagellulæ by the following experiment. He suspended cover-glasses in his aquarium stocked with adult *Polystomellæ*, so that they hung about 2 cm. from the mud layer at the bottom. They were hung vertically (*senkrecht*), and after two days he found 8–15 chambered microspheric *Polystomellæ* (with 1–3 nuclei) adhering to them, and assumed that they had got there by the flagellate swarmspores swimming to them, the amœboid swarmspores being incapable of this amount of locomotion. But he never saw any earlier—more primordial—forms of the organism. I have repeated this experiment in my laboratory at Selsey over two periods of 12 months, hanging the cover-glasses both vertically and horizontally. The glasses are very speedily covered with a mass of Amœboids and Diatoms, among which I have often found young Miliolids, *Polystomellæ*, and *Cornuspiræ*, but in spite of daily observations I have never found a primordial form of any Foraminifer, though I was assisted in the observation for some days in the summer of 1912 by the late Prof. F. GOTCH. We were of opinion that the young forms that we found upon the glasses were carried there by movements in the water which it is impossible to avoid in a fresh sea-water aquarium (brought about by the activity of swimming worms, tiny Crustaceans, Ostracoda, Copepods, etc.), or had fallen upon them from the surface scum (which is always a rich hunting-ground for the young Foraminifera born in the tank), and had attached themselves at once on account of the store of food that they found upon the cover-slips.

³ C. 1901, P., p. 74. "The conjugation of swarmers is a matter of inference rather than of observation, for the process has never been seen." See also *op. cit.*, p. 99. SCHAUDINN's observations upon the flagellisporae had not at that time been published.

⁴ L. 1903, F., p. 72. "Though the zoospores have been seen issuing from their shell, their precise characters when ripe have not been accurately described, nor have we as yet direct evidence as to their fate."

⁵ S. 1903, F.R., p. 551. (In the collected 'Arbeiten,' p. 499 (1911).)

observation of this kind—even when made upon individuals confined within the narrow limits of an observation-cell—presents difficulties which render any exact pronouncement upon the subject, to say the least of it, venturesome. He, however, gives a lengthy and minute description of the process, which was first illustrated in a figure given by LANG¹ which he states was sketched for him by SCHAUDINN for the 'Lehrbuch,' and which is reproduced by CALKINS.² This figure, which shows at a given moment in the life-history of *Polystomella crista* a shell surrounded by bi-flagellate swarmspores, forms part of a hypothetical life-cycle.³ The observations of SCHAUDINN were fortunately confirmed by WINTER, who in 1907 recorded a precisely similar life-cycle in the species *Peneroplis pertusus*, Forskal,⁴ and the process has been succinctly stated by MINCHIN,⁵ who elsewhere points out that syngamy takes place rarely between adult individuals among the Sarcodina, though it has been observed in *Actinophrys*, in *Arcella*, and in *Diffugia*.⁶ It takes place in those species by means of the processes known either as microgamy or macrogamy, and takes place between swarmspores which may be either amœbulæ or flagellulæ. Stated simply, macrogamy is syngamy between full-grown individuals of a species, whilst microgamy is syngamy between the youngest individual products of the rapid multiplication of the adult.⁷

It is, as I have before had occasion to observe, no part of the scheme of this paper to discuss any of the problems of dimorphism, but we may close this section with LISTER's summary:—"The microspheric form terminates its existence by becoming transformed into a number of megalospheric young. The megalospheric terminates its existence by becoming transformed into minute zoospores of uniform size."⁸

The viviparous production of megalospheric young by a microspheric parent has been repeatedly observed in the life-history of *Orbitolites complanata* (Brady) (LISTER, *loc. cit.*), but as we have seen (*ante*) LISTER has recorded that, in the abundance of material at his disposal for the observation of this phenomenon, he found specimens of the megalospheric form containing the megalospheric brood which is usually associated only with parent-shells of the microspheric form.

Before, however, passing from this necessarily faint outline of this branch of the

¹ S. 1903, F.R., p. 552, and A. LANG, 'Lehrbuch der vergleichenden Anatomie der wirbellosen Tiere, vol. 1, Abt. I, Lief 2, 'Protozoa,' 2nd Edit., Jena, p. 208, fig. 210 (1901). (3rd Edit., 1913—in progress.)

² G. N. CALKINS, 'Protozoology,' p. 123, fig. 52, London, 1910.

³ The figure is also given by Dr. RHUMBLER in 'Die Foraminiferen (Thalamophoren) der Plankton Expedition,' Part I, Kiel, p. 324 (1909), with "Schematische Ergänzungen," from DOFLEIN'S 'Lehrbuch der Protozoenkunde,' p. 538, fig. 479, Jena, 1909.

⁴ F. W. WINTER, "Zur Kenntniss der Thalamophoren. I. Untersuchung über *Peneroplis pertusus* (Forskal)," 'Archiv für Protistenkunde,' vol. 10, p. 17, fig. A, Jena, 1907.

⁵ M. 1912, I.S.P., p. 235.

⁶ M. 1912, I.S.P., p. 172.

⁷ M. 1912, I.S.P., pp. 131-2, 172.

⁸ L. 1903, F., p. 73.

enquiry I may be allowed, perhaps, briefly to state an hypothesis which has long been present in my mind, and which may possibly account to some extent for the terrible confusion which exists in the systematisation and nomenclature of the Foraminifera, owing to the universal presence of intermediate forms connecting one species with another—to the despair of systematists. I cannot help asking myself if it is not at least a debatable question whether these intermediate forms are not the results of the union of gametes produced by individuals of different species, giving rise to that process which WEISMANN has called amphimixis, that is to say a mingling of different hereditary tendencies in one and the same individual, an hypothesis which would lead us very simply to the conclusion that when the individuals of a certain species are “constant,” that is to say true to the central type, they have been produced by the conjugation of flagellisporos of the same species, or by amœbulæ as has been described, and that when they are intermediate and untypical they have been produced by the conjugation of flagellisporos (or even—following GODLEWSKI and WALKER—by the fusion of cytoplasm), derived from different species.¹

Thus perhaps has been brought about the bewildering multiplication of superficially unrecognisable species, the specific characteristics of which, in the case of the smaller species, are often only to be revealed by means of exploratory operations—which have, in common with some other exploratory operations, the not infrequent effect of destroying the patient under diagnosis.²

VI. THE THEORY OF REPRODUCTION BY BUDDING.

I come now to one of the main points with which this paper is concerned. That is, that although I am not prepared to say that in no case do two adult individuals “associate” themselves for the purpose (presumably) of reproducing their species, I repeat that this has not been clearly demonstrated, and that the great majority of, if not all, the pairs which we have hitherto been in the habit of describing as “plastogamic” represent a method of reproduction in the Foraminifera which has hitherto, so far as my researches enlighten me, not been seriously put forward, though it was suggested in no uncertain manner by BRADY in dealing with the “double shells” of

¹ A. WEISMANN, ‘The Germ Plasm’ (London, 1893) and ‘The Evolution Theory’ (London, 1904). GODLEWSKI, with whom WALKER agrees, concludes that cytoplasm as well as chromatin must be concerned in the transmission of hereditary characters, that the chromosomes are the bearers of individual characters only, while racial characters may be transmitted by the whole protoplasm of the cell. See C. E. WALKER, ‘Hereditary Characters and their Modes of Transmission,’ London, 1910.

² Since the above was written, this difficulty has to a great extent been overcome in the case of the larger Foraminifera by BARNARD’s application of the X-rays to the examination of the interior structure of the test. In the year 1913 PIERRE GOBY made some experiments in micro-radiography which were recorded in ‘J. R. Micr. Soc.,’ 1913, p. 373, his Plate 17 representing various skiagraphed Foraminifera. GOBY’s skiagraphs, however, cannot be compared with the beautiful results obtained by BARNARD. See note 2 on p. 237.

Textularia folium (Parker and Jones) and *Discorbina parisiensis* (d'Orbigny).¹ The evidence, which is, after all, purely circumstantial, and has only been gathered from observed results, seems to me to indicate that in certain species of the Foraminifera, notably in *Discorbina* and *Bulimina* (though the phenomenon has been observed in a great many other species), the adult organism at a given moment of its life-history forms a new shell from its aperture by the extrusion of protoplasm containing nuclear matter at that point: that this protoplasm proceeds to secrete for itself a shell in precisely the same manner as it would have done if it had been a free amœbula formed of the protoplasm, and discharged from the parent shell, and that this and the subsequent chambers are, in turn, covered with a calcareous investment until the daughter, or budded, shell arrives practically at the adult stage, at which point it casts itself loose and commences an independent existence.

We know that this process takes place in other Sarcodina, notably in *Arcella*,² in *Trichosphærium*,³ and in *Euglypha*,⁴ as an alternative to amœbula and flagellispore production, and it is probable that the Foraminifera in which the phenomenon has been observed likewise vary their reproductive processes. Of these, *Trichosphærium* possesses the greatest interest for us, for it is essentially marine, and it is by the study of this organism in the living condition that the actual course of the process is most likely to be revealed.

So revolutionary a theory as this must be emphasised at the outset by a clear demonstration of the evidence, and fig. 27 (*Discorbina parisiensis*) is put forward in support of the hypothesis. Every rhizopodist who has observed the process hitherto known as "plastogamy" has called attention to the fact that of the associated pairs, one is, in the majority of instances, of strikingly inferior size to the other.⁵

In selecting the specimens for reproduction in fig. 27, I have sought for them only in Dr. J. J. SIMPSON's material from the Kerimba Archipelago, in order that there may be no question as to latitude or environment to account for the disparity in the sizes and development of the associated pairs. It may be remarked that an equally complete series of the same species might have been picked out of the material from Bognor, Sussex, upon which EARLAND made his observations in 1905, or from the Clare Island district, where we noted the occurrence of these associated pairs in considerable numbers and gave a figure of a typical instance,⁶ or, indeed, from any

¹ B. 1884, F.C., pp. 357 and 649.

² M. 1912, I.S.P., pp. 178-9.

³ M. 1912, I.S.P., pp. 182-3.

⁴ M. 1912, I.S.P., pp. 112-3. In the case of *Euglypha alveolata* this process has been most carefully observed and faithfully recorded by GRUBER (G. 1881, T.E., p. 431, Plate 23). Cf. also S. 1874, etc., R., No. 3, pp. 94-104.

⁵ This disparity must of course not be confounded or even compared with the striking dissimilarity in the size of micro- and macrogametes that takes place in anisogamous syngamy in the life-history of other Protozoa. Cf. M. 1912, I.S.P., figs. 69 and 152, p. 172.

⁶ H-A. and E. 1913, C.I., p. 131, Plate 12, fig. 4.

shallow water dredging, or littoral gathering, where the genus *Discorbina* is represented by a wide range of species. If we look at the pair in which the disparity of size is most striking, it will be seen at once that it is, if I may say so, absurd to imagine that a process of "copulation"¹ is taking place between the fully developed adult organism, on the one hand, and the tiny and very elementarily developed individual which is adherent to its aperture in this specimen. Whilst the adult (I allow myself this term and also the term "juvenile" for purposes of definition and demonstration) possesses the full complement of chamberlets which is normal to the species, the juvenile cannot by any means be discovered to consist of more than one very elementary chamberlet, in point of fact, a primordial chamber.² From this point the figures (which, like all other figures illustrating this paper, are drawn from actual specimens and photographs) show a gradual progressional development of the attached juvenile, the size of the adult remaining constant. I may call attention to the fact that (though this species is a very common one, occurring often in relatively enormous numbers in a dredging or a shore-gathering), whether it is found perfect, that is to say, with its base closed in, and delicately striated (which is one of the distinguishing marks of the species), or whether the base is broken away, indicating, in my opinion, that it has been "encysted" or attached—(not adherent)—or whether the neat hole occurs in the base as in figs. 13 and 14, showing the contained young, or revealing a quite empty outer case from which the young have escaped (as in figs. 23 and 24), the size of the species is (within narrow limits) constant, and though it is the commonest incident of one's search, when systematising a gathering, to find in the finest siftings relatively microscopic specimens of forms which one has found large and adult in the coarser siftings, so far as an experience of over twenty years has enabled me to observe, the tiny undeveloped individuals which I am referring to as "juveniles," which might presumably be found seeking their more fully developed "mates," have never been observed—which I think I am justified in saying would have been the case if these associated pairs represented a syngamy of any kind. It would therefore appear that (as I believe to be the case) the "budded off" individual is seldom or never cast loose from its parent until it has attained a practical equality in size, and degree of development. Further, as I have before had occasion to remark, no method of examination, whether by water-immersion with a strong transmitted light, or by mounting in highly transparent media, or by means of the

¹ S. 1895, P.F., p. 189. And see *ante*, p. 242.

² I do not wish to labour this point or to multiply illustrations, but I may mention that, whilst this paper was in course of preparation, I have found in a dredging made in the Timor Sea (50 fathoms) a fully adult individual of *Discorbina pulvinata*, Brady, whose aperture is closed with a tiny individual consisting of two primordial chambers. Now this aperture is situated in the central point of a very deep umbilical recess, and it is absolutely impossible that the primordial shell can have come from outside and attached itself in the apex of this funnel-shaped basal depression.

X-rays, or by careful sectionising of the associated pairs (whether they exhibit practically similar size or a great disparity), has ever revealed any sign of contained "brood." Such a revelation would be, not merely to be expected, but absolutely certain if, at a given moment, the separation of the individuals was destined to lead to the discharge of the young brood, which, as we have seen, was already formed of two, three, or even more calcareously invested chambers.

If we go to the end of the series and look at the equally developed pairs, we see that when this point has been reached the shells begin to separate of themselves. In fig. 27*h* it will be observed that the associated pairs are fully adult. The terminal chamber of the "juvenile" has been formed, and is beginning to raise the flattened bottom periphery of its shell from the similarly flattened bottom-surface of the "adult." All trace of the close and almost homogeneous contact round the edge of the juvenile (which is seen in the earlier stages) has disappeared, and it is obvious that it needs but a very slight disturbance—or jar—to separate the pair into two fully formed individuals.¹

Not to multiply instances, we may take a similar series from a totally different genus belonging to a family far removed from the Rotaliidae in the accepted systematic arrangement of the Foraminifera. Fig. 28 represents a similar series in the species *Bulimina elegantissima* (d'Orbigny). LISTER (to whom, however, this theory has not suggested itself) has given an admirable illustration of two associated pairs of *Bulimina elegantissima*, var. *semi-nuda*, from Delos.² In this series of *Buliminae* the disparity which I adduced in support of this theory is even more striking, regard being had to the shape of the shell, than in *Discorbina*. The juvenile in the first pair of the series is almost more ridiculously minute than in the first of the *Discorbina* series, consisting, as before, of no more than one tiny chamber—the first formed of the developing juvenile—extruded from the orifice of the adult shell.

In the species *Bulimina elegantissima*, adult shells are often found, the base of which has been absorbed or dissolved away, suggesting strongly the appearance of the frequently found empty shells of *Discorbina* (figs. 23 and 24), but in no instance have I ever been able to trace any appearance of viviparous young, in the adult shells, thus resorbed after (?) separation, either by breaking them apart, or by

¹ *Vide ante*, p. 242. In the earliest stages of this process of budding, the primordial and earliest-formed chambers are so closely adherent to the adult shell that they appear to be cemented together, an appearance which, though it must not be confounded with the detritus which in certain cases accumulates around the badly fitting bases of associated pairs—presenting a different phenomenon—doubtless conveyed to SCHAUDINN the impression of a secondary shell-substance, uniting the pair.

² L. 1903, F., p. 126, fig. 54. The originals of this figure were from the collection of Mr. SIDEBOTTOM, who calls attention (S. 1904, etc., R.F.D., 1905, p. 11, Plate 2, figs. 7–12, and Plate 3, figs. 1, 2) to the great frequency of this phenomenon of association in this species. Mr. SIDEBOTTOM has kindly lent me his Delos specimens, of which I have made use in this place.

careful sectionising whilst in the associated or "budding" condition.¹ A certain degree of resorption of the internal septa is frequently to be observed, as in *Discorbina*, but I am of opinion that this is sometimes a natural consequence of the budding, and that this expenditure of shell matter of the adult may be made good after the separation of the pairs, when the juvenile has reached the adult stage, and at others represents the exhaustion of a parent shell after discharging its amoebulae or flagellipores.²

The same phenomenon is of common occurrence in the species *Discorbina pileolus* (d'Orbigny), and BRADY figures the process very clearly.³ EARLAND and I have made several sections of associated pairs of this species, with the same negative results as in the case of *D. parisiensis* and *Bulimina elegantissima*, as regards contained young, but we have found at least one glauconitic cast of a pair in the same kind of association as SCHAUDINN observed in *Patellina corrugata*, in which the protoplasm of two adult parent shells, set eccentrically to one another (as in SCHAUDINN's figure), is extruded between and beyond the concave bases of the shells, and is, in my opinion, at the point in its history at which the protoplasm is about to break up into amoebulae as in the cases of *Polystomella crispa* observed and figured by LISTER (*vide ante*). This specimen is not, I take it, to be confused with the entirely independent process of "budding," which is frequently to be observed in the species.⁴

This "association," whether it be fortuitous or the result of "budding," must be very carefully distinguished from the phenomenon of double shells, that is to say, shells which either at the commencement of their life have started, or later in life have developed, as twins of the attached or Siamese variety. The latter, an instance of which in the genus *Textularia* (dredged by Prof. HERDMAN) is shown in fig. 29, I am inclined to look upon as a deformity arising most probably from damage to the living organism (which it has repaired in the manner familiar among Foraminifera), and to which, especially in the case of *Orbitolites* and *Miliolina* (*post*), reference is

¹ We are publishing a series of such shells with "resorbed" terminal chambers in our Kerimba monograph in the 'Transactions of the Zoological Society' (1915, Plate 48, figs. 26-29).

² This absorption of internal septa has been noted in many species in connection with which no suggestion of "plastogamy" has ever been made. Notably in the genus *Polymorphina*, in which the phenomenon was made the subject of minute research by the late Dr. ALCOCK ('Proc. Lit. and Phil. Soc. Manchester,' vol. 22, p. 67 (1883)). SIDEBOTTOM has also referred at some length to this feature in *Polymorphina*. (S. 1904, etc., R.F.D., 1907, p. 17.)

³ B. 1884, F.C., Plate 89, figs. 2-4.

⁴ A convincing instance of this is afforded by figs. 25 and 26, which represent perfect glauconitic casts of the protoplasmic bodies of two individuals thus associated. Here we have clear demonstration of the perfect condition of the associated animals, of the complete septation of the interior of their shells, and of the protoplasm connecting the two shells, forming a "pad" between them, and which is *not* part of the protoplasm of either withdrawn from the shell. The specimens come from a dredging in 60 fathoms off "Poor Knights," New Zealand.

made in this paper.¹ In the former case, a striking instance of which is seen in fig. 30, in the case of the species *Bulimina elegans*,² it seems impossible to account for these shells save by an accidental fusion of the amœbulæ from which they started. Whatever circumstances in their earliest independent stage of life caused them to adhere, it is clear that they were unable to get away from one another before the first chambers had become covered with a calcareous investment, after which it was, of course, impossible.³

This is not a phenomenon which is confined to the polythalamous forms; it is not uncommon to find monstrous pairs of Lagenæ having two apertures, which are true Lagenæ and not merely biloculine Polymorphinæ.⁴ The specimen of *Lagena lucida* which we figured in our Selsey monograph⁵ presents another and perhaps more obscure phenomenon, for there the base of the one shell was firmly attached to the

¹ These "monstrosities" must not be confounded with the phenomenon of "multiformity," the admirable definitive term used by LISTER for those Foraminifera (for which in some cases genera have been instituted, *e.g.*, Bigenerina, Spiroplecta, Amphicoryne, etc.), in which "the plan on which the chambers are arranged in the growth of the test, changes in the course of growth." (L. 1903, F., p. 58, etc.) I am anxious in this paper to avoid any discussion of the phenomena associated with dimorphism properly so called, and I do not propose to do more than touch upon these "multiformities" in passing, but I may say at once that I entirely agree with LISTER in ascribing great biological significance to these forms. They have hitherto been called "dimorphic forms," but the term "dimorphism" having now come to be used to describe an important condition of the life-history of nearly all (if not all) Foraminifera, his term "multiform" becomes extremely lucid and useful, and is preferable to RHUMBLER's suggested terms "biformed" and "triformed." (R. 1895, N.S.T., p. 63.) LISTER has pregnantly observed that for the most part megalospheric individuals are uniform, and microspheric are multiform in the Miliolidæ, and calls attention to the hitherto little regarded multiformity of such genera as Orbitolites (primordially Peneropline) and Polytrema (primordially, Rotaline and free), and so on. He also sets forth the views of RHUMBLER (with whose conclusions, however, he disagrees, for reasons stated), that "in the multiform tests the early chambers are arranged on a higher (*i.e.*, a more resisting) plan than those added later," from which RHUMBLER, like CARPENTER, gathers conclusions of a high biological significance (*loc. cit.*, pp. 89, 135, 137, 140). We cannot go into this important subject in a cursory manner in this place, but I figure an interesting specimen of *Hauerina compressa*, d'Orbigny, which has extravagated into a peneropline chamber. (Fig. 31.) Similar extravagances have been observed in the genus Polystomella.

² Figs. 29 and 30 are drawn from specimens dredged in 1913 by Prof. W. A. HERDMAN in Loch Sunart (12 fathoms). We figured an exactly parallel case in the genus Polymorphina in our Clare Island monograph (H-A. and E. 1913, C.I., Plate 8, fig. 16). In that instance the two shells are joined by their *initial* chambers and grow outwards just as in the *Bulimina* (fig. 30).

³ With such phenomena as this may be compared the bifurcated monstrosities (*Spaltungsmonstrum*) in the genus Peneroplis, figured by RHUMBLER on Plate 12 (fig. 13) of his 'Foraminiferen der Plankton-Expedition,' Plate 1 (Kiel, 1909). BEISSEL (B. 1891, A.K. Atlas, Plate 3) has figured an elaborate series of these monstrosities in his genus *Lituola aquisgranensis*.

⁴ Some remarkable instances of this phenomenon have been figured by more than one rhizopodist, and notably by SIDEBOTTOM, who figures such twins and triplets of *Lagena striata* (d'Orbigny) from Palermo. ('Proc. Manchester Lit. and Phil. Soc.,' vol. 54, Plate 2, figs. 1, 2 (1910).)

⁵ H-A. and E. 1908, etc., S.B. 1911, p. 318, Plate 10, fig. 16.

apertural end of the other. We suggested in that place that this abnormality was probably due to budding, and it is conceivable, though not so probable as in the other case, that this is due somewhat to the same process as the budding-off of young which I have illustrated in connection with *Discorbina* and *Bulimina*. Fig. 32 represents similar pairs of the species *Lagena costata*, *squamosa*, and *williamsoni*. In the latter instance (fig. 32a) the parent shell is *Lagena williamsoni* and the daughter-shell *Lagena costata*, which affords an excellent illustration of the little value of so-called specific differences in the Foraminifera. (*Vide post*, p. 262, concerning the genus *Miliolina*, and *cf.* B. and W. 1885, D.I.S., Plate 14, where the same three species are figured in this condition.) Before leaving this matter, it may be observed that specimens of *Orbitolites* commencing with two primordial chambers side by side are far from uncommon; fig. 33 represents a specimen showing the co-operation of five (or six?) primordial chambers, all megalospheric, and Mr. LISTER informs me that this is a phenomenon which he also has observed in material from the Pacific Ocean.

As a concluding illustration of this matter of multiform shells, and before turning to the history of *Cymbalopora*, it will, I think, not be uninteresting to give a figure of a very remarkable multiformity the origin of which may be said to be more than obscure. Fig. 34 represents an organism found in a dredging sent to me by Prof. HERDMAN from Loch Sunart, on the West Coast of Scotland (dredging 12 fathoms, July, 1913). In this shell the commencement is typically Rotaline or Globigerine, but after forming two convolutions, the animal has suddenly turned into *Nodosaria scalaris* (Batsch) of the variety to which O. SILVESTRI has given the specific name *proxima*.¹ How this is to be accounted for I am absolutely at a loss to imagine, unless it is to be explained by WEISMANN'S theory of amphimixis, to which I have alluded above, in this case syngamy having apparently taken place between gametes derived not from individuals merely of different genera or species, but from individuals of entirely distinct sub-families. Similar multiformities combining genera (*e.g.* *Cristellaria* and *Polymorphina*) of the same sub-family are not uncommon.

The conclusions to which I have been brought by the considerations set out in the foregoing pages are, shortly, as follows :—

(1) That in certain species of the Foraminifera (whose number will be increased as research is pursued along these lines) reproduction takes place (in addition to the zoospore method of production as observed by LISTER and others) by viviparity, and by budding-off of young individuals.

(2) That viviparous young are formed inside the parent shell, and that these young emerge from the parent by dissolution of the base of shell.

(3) That the whole of the protoplasm and internal septa of the parent are used up in this process, whereas in zoospore production the protoplasm only is discharged, the shells of the young being secreted outside the parent, from material derived from the surrounding medium, and not from the internal septa.

¹ O. SILVESTRI, 'Le Nodosarie fossili e viventi, etc.,' Catania, 1872, p. 63, Plate 6, figs. 138–147.

(4) That at certain stages of the life-cycle (as in *Arcella*) a young individual is budded off from the aperture of the parent and set free at maturity.

(5) That under certain (possibly fortuitous) circumstances, the protoplasm extruded from two or more shells mingles, as in SCHAUDINN'S observations, preparatory to the formation of embryonic shells outside the parent as described by LISTER.

(6) That the phenomenon hitherto described as "plastogamy" in the Foraminifera is generally attributable to one or other of these last two processes.

VII. ON SOME NEWLY OBSERVED PHENOMENA IN THE LIFE-HISTORY OF THE GENUS CYMBALOPORA.

(a) *On Cymbalopora bulloides, its Internal Structure and Variations.*

The late Sir JOHN MURRAY,¹ who probably devoted more attention and thought to the study of the pelagic Foraminifera than any other marine biologist, pointed out that "the pelagic Foraminifera play a most important role in the economy of the present ocean as well as in the geological history of our planet,"² calling attention to the fact that their dead shells account for a deposit of unknown thickness covering approximately fifty millions of square miles of the floor of the existing oceans, over 90 per cent. of which consists of carbonate of lime derived from their dead shells.³ The study of the pelagic Foraminifera is one involving questions of the highest oceanographical importance, and the problems involved in their distribution are far from being solved at the present day. But among these pelagic forms there is one which is common in shallow tropical seas, especially in the vicinity of coral islands, whose life-history presents some features which have not been observed in connection with any other Foraminifer, and whose protoplasmic body has recently been discovered to be endowed with functional activities never yet observed in the group. Sir JOHN MURRAY stated that the most familiar species of the family, *Cymbalopora bulloides* (d'Orbigny) (fig. 35), can hardly be regarded as a true pelagic Foraminifer,⁴ but I think it is made clear by the researches which I am taking this opportunity of recording, that *Cymbalopora bulloides* represents a definite pelagic stage of more than one well marked Rotaline genus, and though it is convenient for purposes of systematisation to retain the species *Cymbalopora bulloides*, it is more than probable that the distinctive feature of a large balloon-shaped, highly perforate, terminal chamber, connected with the earlier chambers at its peripheral margin, and filled with the

¹ See Note, p. 227.

² M. 1897, P.F., p. 17.

³ M. 1913, O., pp. 205-7. Sir JOHN MURRAY has here recorded that Globigerina ooze accumulates at a rate of about an inch in the year in 2300 fathoms, and at a somewhat more rapid rate at lesser depths. Calculating upon practically similar data, JUKES-BROWN ('Handbook of Physical Geology,' London, 1884, p. 130) estimates that the English chalk was deposited in a sea of a depth of not more than 500 fathoms over a period of 150,000 years.

⁴ M. 1897, P.F., p. 20.

protoplasmic body, and containing moreover an inner chamber *not* so connected and normally quite empty, to which EARLAND has given the name of the "float-chamber," is assumed at certain stages of their life-history by certain species of the genera *Discorbina* and (?) *Planorbulina*.¹ It is further to be observed that in all *Cymbalopora* gatherings the typical form *Cymbalopora bulloides* divides into two well marked classes, a large and relatively robust form (fig. 35*a, b, c*), and a small and more delicate form (fig. 35*d*). KEMNA, who had evidently not seen EARLAND's paper upon the genus,² writing upon the Pelagic Foraminifera in 1903, appears to have no doubts upon the significance of this phenomenon. He says (after quoting Sir JOHN MURRAY) that :—" Arrived at a certain size the individual sporulates ; with this object in view the protoplasm massed into the umbilical depression swells and secretes the balloon-chamber ; the animal floats : these are the small individuals of the plankton. After discharging the spores (by rupture of the balloon ?) the animal sinks to the bottom and starts growing again ; after some time it sporulates again, floats, and now constitutes the large individuals of the plankton."³ The dual nature of the terminal chamber had entirely escaped him, and his categorical statement upon these phases in the life-history of the organism does not appear to be founded upon any observations made upon the living animal, or to be supported by any direct evidence.

Additional evidence that this balloon-chamber represents a stage in the life-cycle is afforded by the presence in all gatherings of *Cymbalopora* of a variety for which we propose the specific name *milletti* (fig. 36) which was first figured by MILLETT from DURRAND's gatherings in the Malay Archipelago.⁴ EARLAND's observations, recorded in the year 1902, were made upon a sample taken from a band, 5 inches broad and extending over a quarter of a mile, along the ripple margin on the shore of Corny Point, Yorke Peninsula, S. Australia, in 1880. This deposit (which was carried away by the next tide, and, though carefully searched for, was never seen again), consisted of countless myriads of pure *Cymbalopora bulloides*, and a strewn slide of the material just as it was taken (fig. 37) is practically indistinguishable from two slides sent me by Sir JOHN MURRAY containing this organism taken in tow-nets on the surface (February 2, 1875) off Zamboanga in the Philippine Islands, and (August 2, 1875) off Honolulu in the Sandwich Islands (fig. 38). The latter gathering, mounted fresh from the surface, consists of nothing at all besides

¹ This balloon-chamber varies from a quite spherical to a flattened globe, or a thin compressed chamber ; these latter probably represent early stages of the balloon-chamber. In extreme cases (fig. 39*a, b*) the balloon is merely a relatively small sub-conical excrescence added below, and closing in, the rotaline portion. This may, however, be merely an immature, or growing, or even a deformed and abnormal balloon-chamber.

² E. 1902, C.B.

³ A. KEMNA, "Les Caractères Structuraux de la Coquille des Foraminifères Flottants," 'Ann. Soc. Roy. Zool. et Malacol. de Belgique,' vol. 38, pp. 109-127 (p. 124), (1903).

⁴ F. W. MILLETT, "Report on the Recent Foraminifera of the Malay Archipelago Collected by Mr. A. Durrand," 'J. R. Micr. Soc.,' Part XV, p. 697, Plate 7, fig. 4 (1903).

C. bulloides in all its types. The species, first described by D'ORBIGNY in 1839,¹ received no further notice until KARL MÖBIUS devoted a considerable amount of attention to it under the name of *Tretomphalus bulloides* from material gathered in Mauritius and the Seychelles,² and his generic name *Tretomphalus* (which has not been retained) called attention for the first time to one of the leading features of the shell, the depressed "navel" leading to an entosolenian tube, which occupies the centre of the terminal (or balloon) chamber, among the coarse and characteristic perforations, a feature which entirely escaped the attention of D'ORBIGNY, though he particularly sought for a definite aperture.³ In many of our Kerimba Archipelago specimens the entosolenian tube terminating inside the float chamber is crowned with a kind of "crown" of more or less highly developed spines (fig. 40).

It was EARLAND, in the year 1902, who called attention to the fact that this umbilical entosolenian tube was not an opening of communication between the protoplasmic body of the organism and the surrounding medium, but communicated directly with the corresponding umbilical tube of a lobulated inner chamber which he described as a "float-chamber" which, in the vast majority of specimens observed, is absolutely empty.⁴ A careful examination of a very large number of specimens, made by the delicate operation of dissecting off, first the outer balloon-chamber (fig. 41), and then the inner float-chamber (fig. 42), and also by sections of the whole shell down the median plane (fig. 43), shows that the latter has no perforations connecting it with the rotaline aboral portion of the shell, and it becomes an extremely interesting problem whether or not this float-chamber can be filled at will by the organism with air (or gas) for the purpose of raising it to the surface water of the ocean, or in turn with water for the purpose of sinking it to the bottom.⁵

¹ *Rosalina bulloides*, d'Orbigny, "Foraminifères" in RAMON DE LA SAGRA'S 'Histoire Physique, Naturelle, etc., de l'île de Cuba,' Paris, p. 98, Plate 3, figs. 2-5 (1839).

² K. MÖBIUS, "Beiträge zur Meeresfauna der Insel Mauritius und der Seychellen," 'Foraminifera von Mauritius,' Berlin, p. 98, Plate 10, figs. 6-9 (1880).

³ It must be admitted that this entosolenian tube is often very obscure, and in the small Corny Point specimens EARLAND often found very great difficulty in establishing the existence of any entosolenian tube at all.

⁴ E. 1902, C.B., p. 315. "It occupies nearly the whole of the interior of the balloon, in which it hangs suspended, but is not attached to the inner surface of the balloon in any way. It is attached to the lower surface of the upper or spiral shell, but it has no direct connection with these upper chambers, the only opening into its interior consisting of the small tube in the centre of the base discovered by MÖBIUS. This tube is not in any way connected with the external or balloon chamber, the inner surface of the base of the balloon being perfectly smooth except for the large "orbuline" pores. In shape the chamber varies considerably in different specimens. In the Corny Point specimens, and in most small shells, it is almost perfectly globular, and exhibits none of those constrictions which are characteristic of the float-chamber in larger mature shells." The same remarks may be made with regard to Sir JOHN MURRAY'S Philippine and Sandwich Islands surface specimens.

⁵ The existence of gas-vacuoles apparently having this object has been established by different observers in many of the Sarcodina, especially in such forms as *Arcella* and *Diffugia*, which exhibit so many attributes held in common with the Foraminifera. (C. 1901, P., pp. 89, 90.)

It is, however, to be observed that in some instances this float-chamber in turn is filled with a yellow granular substance which brings the float-chamber into very prominent relief (as independent of the balloon-chamber) when specimens are mounted in transparent media (fig. 44). Sir JOHN MURRAY records that among his specimens not a single one contained ordinary protoplasm such as is found in the shells of other Foraminifera.¹ He refers, of course, to the large terminal chamber as a whole, the dual nature of which did not impress itself upon him, although the figure which he gives (which had already appeared in BRADY's monograph²) clearly suggests it (fig. 45), the rotaline initial portion of the shell being always filled with a deeply coloured protoplasm. But Sir JOHN MURRAY also records a very remarkable fact, that in all his specimens the shells, *i.e.* the terminal chamber, were "filled with immense broods of minute zoöspores, and that these latter spread over the field of the microscope in a cloud-like swarm when a shell was broken under the cover-glass."³ Before speculating upon the significance of this phenomenon, it may be observed that the disposition of the float-chamber presents a marked difference in the species *C. milletti*. In this species (figs. 36 and 46) the balloon-chamber, instead of being smooth and coarsely perforate as in the normal type, is strongly *wrinkled*, and moreover appears to be slightly constricted into four distinct lobes, as if it had been twice tied across in the ordinary manner of a soft parcel.⁴ It is very difficult, and frequently impossible, in this variety to differentiate the float-chamber from the balloon-chamber; the lobulate outer wall of the float-chamber adheres closely to the smooth or wrinkled inner wall of the balloon-chamber, the only open spaces between them being formed by the independent and somewhat more marked constriction of the float-chamber lobulations (fig. 47), which, in broken specimens, are frequently seen

¹ M. 1897, P.F., p. 20.

² B. 1884, F.C., p. 639, fig. 20. It is not a little remarkable that the existence of this float-chamber should have escaped both Dr. BRADY and Prof. MÖBIUS. Both of them state in definite terms that the final balloon-chamber is single, but both of them show the inner chamber very distinctly in their figures. We can only assume that they both regarded it as being merely a thickening of the wall of the balloon-chamber.

³ This statement, surely one indicating a phenomenon of the highest biological importance, has been baldly repeated without comment (except of a misleading kind), and without further investigation, by nearly all writers upon the Foraminifera since BRADY first quoted it (over Sir JOHN MURRAY's initials), as a footnote on p. 639 of his "Challenger" Report. By the courtesy of Sir JOHN MURRAY I have been privileged, not only to see all the slides of *Cymbalopora* mounted by him on board the "Challenger," but to read and extract all the observations on the phenomenon contained in his laboratory note-books kept on the cruise. These are of so great an interest and significance, that with his permission I have set them out in an Appendix A to this paper.

⁴ To a certain modified extent it resembles in contour the contained float-chamber, which as EARLAND (*loc. cit.*, p. 315) says: "bears some resemblance to a tomato or to a bag of wet sand tightly bunched together at the top." In this variety the balloon is nearly always broader than the rotaline commencement (see fig. 36a), the maximum diameter of the whole shell occurring at, or just above, the base of the balloon-chamber, which shows the same tendency as in the normal type to a greater or less degree of depth or compression.

to take the form of hollow triangular "struts" or pillars, disposed around the outer circumference of the terminal chamber and running up to the rotaline portion (fig. 48).¹ Seen under a high magnification ($\frac{1}{5}$ inch, 5 mm.) these "wrinkles" are seen to be due to thickened and curved lines of shell-matter which are adherent between the inner surface of the balloon-chamber and the outer surface of the float, but it is not clear to which chamber they belong if they are not homogeneous.² In Sir JOHN MURRAY's slides from Honolulu (August, 1875) there are many extremely hyaline specimens of *Cymbalopora milletti*, in which there appears no trace of any duality or distinction between float and balloon in the terminal chamber, which, though highly lobulate, is only very sparsely "wrinkled." It may also be observed that whereas in the normal type (*C. bulloides*) the chamberlets which form the commencement of the shell are invariably Rotaline (fig. 49) (as in *Discorbina concinna* and *Discorbina mediterraneensis*), and, apart from the terminal balloon-chamber, are indistinguishable from *Discorbina*, that portion in *C. milletti* is almost invariably acervuline (fig. 50), the chambers being heaped into a more or less pronounced cone after a small rotaline commencement, which is obscure or plainly marked according to the individual specimen.³ It may also be noted that, whereas in the normal type there is usually a pronounced constriction where the rotaline portion joins the balloon-chamber, in *C. milletti* the junction is almost invariably flush with the immediately broadening balloon (fig. 50). For this reason I am inclined to express the opinion that *Discorbina concinna*, Brady (which BRADY himself considered was "possibly only the immature or arrested stage of some better known species"⁴), is, as a fact, the immature or arrested stage of *Cymbalopora bulloides*, whilst *Discorbina mediterraneensis* (d'Orbigny) is the immature or arrested stage of *C. milletti*, passing through a stage which has been separated and diagnosed as *Cymbalopora poeyi* (d'Orbigny), or (to put it in another way) that *Discorbina concinna* and *Discorbina mediterraneensis*, at some stage in their life-history, proceed to the formation of the balloon- and float-chambers with a view to adapting themselves to a pelagic existence,⁵

¹ These triangular "struts" appear occasionally to be set free in the interior of the float-chamber, as in the figure, by the growth of the chamber beyond them.

² One of our specimens shows what appears to be a young four or five chambered Rotaline embryo inside the float, and many small highly transparent spherical bodies equalling in diameter a single chamber of the young (?) individual (fig. 51). For reasons, however, presently to be set forth I hesitate to say that these are embryonal forms, though the apparently perfect embryo-shell contains a small dark mass which may represent the nucleus. Somewhat similar dark masses are visible on other portions of the interior of the balloon, especially between the lobes of the float, but I am inclined to think that these are metaplastic bodies of various kinds—stercomes? or symbionts?—but possibly nuclei.

³ It must be noted that there is also a somewhat rare form of the typical *C. bulloides* in which, as EARLAND has recorded (E. 1902, C.B., p. 318, Plate 16, figs. 3, 4), "the early chambers are . . . so largely developed that the balloon is entirely hidden when the spiral portion is uppermost."

⁴ B. 1884, F.C., p. 646.

⁵ Cf. SIDEBOTTOM's figure of *Bulimina elegantissima* with an excrescent balloon-chamber closing in the base of the shell. S. 1904, etc., R.F.D. 1905, p. 12, Plate 3, fig. 2.

Cymbalopora poeyi being an exaggerated and highly lobate form of *Discorbina mediterraneensis* with a deep umbilical depression (fig. 52).¹

I do not think that the specimens which we have found, in which the float-chamber is filled with a dark granular mass (shown in fig. 44), can be specimens containing dried remains of the monadiform bodies described by Sir JOHN MURRAY, though it is to be remarked that in many of the slides of *Cymbalopora bulloides* netted from the surface, in connection with which Sir JOHN MURRAY describes this phenomenon, the granular contents of the float-chamber are quite as pronounced as in our Kerimba Archipelago specimens, especially in the tow-nettings of July 27, 1875, made in Honolulu Harbour, where a clear and empty "float-chamber" is rather an exception. I have had no opportunity like Sir JOHN MURRAY of examining these organisms when freshly caught, but I have little doubt that the "monadiform bodies" described by him were expressed from the outer periphery, *i.e.* from the space between the float-chamber and the balloon-chamber, and that the coloured granules observed in the float-chambers of the specimens to which reference has been made are microscopic algæ (Xanthellæ). In several specimens after the removal of the balloon-chamber (fig. 42) the inner surface of the very hyaline float-chamber has been seen to be dotted with minute black or brown specks, which we at first thought might be the dried remains of Sir JOHN MURRAY's monadiform bodies, but on reflection it seems almost certain that these minute bodies are the desiccated Xanthellæ. These views are supported by the fact that these Xanthellæ, which are surface organisms, have been observed in other pelagic forms, and notably in *Globigerina*.²

We have never observed any traces of protoplasm in the float-chamber, but the space between it and the inner surface of the balloon-chamber is frequently filled

¹ GOËS, following BRADY no doubt, considered *C. bulloides* to be merely a modified *Discorbina* (G. 1882, R.R.C.S., p. 106, Plate 8, figs. 262-3, and G. 1896, F.A., p. 70). I do not propose in this paper to offer any observations upon *C. poeyi* (d'Orbigny). It is a highly variable species and in many cases is undoubtedly merely *C. bulloides* (typical, or var. *C. milleti*) before it has acquired the balloon or after it has lost it. Among Sir JOHN MURRAY's specimens from Honolulu (July 27, 1875) there are many individuals, the initial portions of which, as seen through the "balloon," are typically *C. poeyi* of the most highly lobulate type, occurring side by side with the broad Planorbiline, and the neat Discorbine, types, and also typical *C. poeyi* without any trace of the balloon. The number and shape of the lobulations on the under (or umbilical) surface is very variable, depending upon the number and size of the individual chambers of the shell. The colour varies from pure white, to a deep brown owing to the contained protoplasm, which is frequently as dark as in *Discorbina mediterraneensis* (d'Orbigny) and others of that group.

² M. 1913, O., p. 149. The importance of these microscopic algæ which float everywhere within the photic zone in countless myriads cannot be overestimated. MOSELEY has recorded the occurrence of these Protophyta in immense quantities in the surface waters of the sea between Ternate and the Philippine Islands, where, as we have seen, *Cymbalopora* was taken in vast numbers in the tow-nets by Sir JOHN MURRAY. (M. 1879, N.N.C., p. 567.) He (MOSELEY) also calls attention (*loc. cit.*) to the importance of these unicellular algæ in the economy of pelagic life.

with dry protoplasmic *débris*. This assumes very varied and fantastic shapes, so much so that I hesitate to suggest that the apparent embryonic Rotalian referred to above, and seen in one of our specimens occupying this space, is a young shell of the species in the rotaline stage—but its appearance (fig. 51) is very striking; it is, unfortunately, so far as I can discover, unique, and therefore to be regarded with caution.¹ If any trace of protoplasm were to be found in the float-chamber its presence would be, to say the least of it, enigmatic, for the float-chamber is, as I have observed (*supra*), entirely sealed off from the rotaline portion of the organism.

EARLAND² has suggested that Sir JOHN MURRAY's monadiform bodies were zoöspores, and that being discharged (in the normal life-history of the organism) either through the "orbuline" pores at the base of the balloon-chamber, or, more probably, by the rupture and dissolution of the balloon, the discorbine and acervuline portion of the animal need not necessarily perish, but might continue its existence—the discorbine specimens (typical *C. bulloides*) in my opinion as *D. rosacea* (or *D. concinna*), and the acervuline specimens (*C. milletti*) as *Discorbina mediterraneensis*, or as *Cymbalopora poeyi*.

(b) *On Cymbalopora tabellæformis as an Excavating Foraminifer.*

Wherever *Cymbalopora bulloides* and its associated form *C. milletti* are plentifully found as shallow-water littoral-zone forms, they are accompanied by a very distinctive species known as *Cymbalopora tabellæformis*, Brady, the prominent feature of which, as its name implies, is a flat superior surface, on the coarse "platform" of which, one end of all the chamberlets are visible (fig. 53). The outline of the shell may be circular, or oval, and the rotaline commencement is often very pronounced, in some of the Kerimba specimens showing as many as 12 rotaline chambers before the annular or acervuline method supervenes.³ It never terminates, so far as we can judge, from the great mass of material which we have examined, in a balloon- or float-chamber. The chamberlets forming the outer annulus (which are exceedingly numerous) curve downwards towards a deep umbilical depression (somewhat suggesting the claw-like tuber of the garden *Ranunculus*), and the distinctive feature of these outer chamberlets consists (as is very clearly seen in BRADY's figure)⁴ in the multiple aperture of the organism which takes the form of

¹ CHAPMAN (C. 1902, F., p. 217) speaks of "the frequent occurrence of embryonic shells living within the balloon-like chamber, which are liberated through an entosolenian orifice." This statement is made without any reference or authorities, and is, in our opinion, unjustifiable. CHAPMAN must, we think, have been alluding to the oft-quoted reference to Sir JOHN MURRAY's "monadiform bodies."

² E. 1902, C.B., p. 320.

³ The typical shell is very distinctive in appearance, but the species shows a large range of intermediate forms linking it by imperceptible stages with *Cymbalopora poeyi* (d'Orbigny). The older the shell, the thicker and coarser is the appearance of the "platform."

⁴ B. 1884, F.C., Plate 102, figs. 15–18.

a number of large perforations along the lines of the sutural depressions of these chambers.

Among the coarse material from one of the stations in the Kerimba Archipelago we have found some specimens of this species presenting a phenomenon which, so far as my knowledge goes, has never been observed in connection with any other Foraminifer or, indeed, with any other of the Protozoa. In certain relatively large calcareous fragments (apparently derived from bivalve mollusca, and more or less thickly encrusted with nullipore algæ), we have found a number of specimens of *Cymbalopora tabellæformis* sunk into cavities in the shell in a manner strongly reminding one of the "crypts" occupied by *Pholas saxicava* (fig. 54). The superior surfaces of the *Cymbaloporæ* are sunk slightly below the surface of the molluscan shell, and the visible edges of the crypts slightly overlap the *Cymbaloporæ*, showing that the animal has grown in diameter since it encysted (or encrypted?) itself. This is further proved by the occurrence of specimens of very different sizes ranging from a superior visible diameter of 0·2 mm. to 0·5 mm. A specimen (fig. 55) was removed by being carefully dug out with a needle, and it was then found that it loosely occupied a cavity (or crypt) exactly the size of the test. Most of the chambers of this removed specimen were found to be filled with a yellowish-green granular matter which, though the specimens were dead and dried, appear to me to be Xanthellæ in all respects similar to those described as colouring the protoplasmic bodies of Orbitolites by MOSELEY at Tongatabu.¹ Round the inside of the crypt are set the circular openings of several radiating passages which extend in all directions into the substance of the molluscan shell, obviously for the accommodation of the extruded pseudopodia of the Foraminifer (fig. 56). In some cases where the surface of the mollusc has been rubbed away and the *Cymbalopora* has become dislodged and has disappeared, the rubbing away has reached these passages, so that it is possible to trace their extent. It is possible, though not probable, that the animal may cut grooves radiating over the surface of the shell, whilst it is occupying its crypt, but the former—the burrowing from inside—is the more likely hypothesis. The molluscan fragments containing these *Cymbaloporæ* which we found were only two in number (though they contained as many as 10 specimens of the organism, *in situ*, and nine empty crypts), and therefore I have hesitated to destroy them by sectionising either of the fragments with a view to discovering whether these passages (or tunnels) anastomose with one another, or with the radiating passages of their nearest neighbours—though some of the surface striæ (laid bare as described) convey that impression, and I have not been able to identify on the surface of the molluscan shell any points of emergence. Exception being made of the relatively large openings of these passages, the interior of the crypts is quite smooth, and not lobulate like the chambers on the sloping, or claw-like, periphery and underside of the foraminiferal test, which would indicate that the animal has some limited scope of

¹ M. 1879, N.N.C., pp. 292–3.

rotatory movement inside its crypt. In some of the crypts which we found empty, tunnels led downwards from the bottom of the crypt as well as outwards from the periphery (fig. 56).

When first we observed these empty pits, we concluded, not unnaturally, that they were due to the ravages of boring algæ, such as the various species of the genera *Lacuna*, or *Achyla*,¹ or of minute examples of the boring sponge *Cliona*, but this question was settled by the discovery of the encrypted Foraminifera. Now the question before us is: By what agency or property of the protoplasm of these animals are these crypts hollowed out in the first instance, and the tunnels subsequently bored? If the organism were an arenaceous form or endowed in any way with siliceous granules (as in the case of *Cliona celata*, Grant) it would be reasonable to assume that they were bored by mechanical means, and we should then find in the crypts and tunnels, when specimens were newly dug out of them, calcareous particles such as were observed by HANCOCK in the case of that organism.² But I think there is no doubt that we are here in the presence of a very remarkable functional development of the solvent action of the foraminiferal protoplasm. It is not unreasonable to suppose that the same power which enables the Foraminifer to secrete a calcareous test enables it to dissolve, not only its own test [as has been suggested (*post*) in discussing the growth-process of the calcareous *Monothalamia*], but also the calcareous shell of the mollusc in which it desires to burrow, and it is not improbable that the thick and robust test of *Cymbalopora tabellæformis* is due to this abnormal power of utilising calcareous matter, and assimilating it, not only from its environmental medium, but also from its host. Another possibility which has been suggested to me is that the infinitesimal amount of carbonic acid produced by the digestive processes of the organism itself, or resulting from the activities of the symbiotic *Xanthellæ* in the elaboration of their chlorophyll, might in time act as a solvent upon the host-shell, and thus accommodate the growing guest, but I think that the more likely explanation is to be found in an actual and direct solvent power of the protoplasmic substance of the animal.

¹ A very full and interesting account of these Thallophyta is contained in W. H. HARRIS'S "Notes on a Group of Marine Microscopic Vegetable Organisms, invading Calcareous Organic Remains" ('J. Quek. Micr. Club,' Ser. 2, vol. 7, pp. 138-161). It frequently occurs in littoral gatherings, containing any marked proportion of dead shells, that we find many of the Foraminiferal tests riddled in all directions by these boring algæ, which attack the organisms in all clean shell sands. Shells from muddy dredgings are not so liable to attack, the investing mud appearing to afford a protection from their ravages. (Cf. L. RHUMBLER, 'Foraminiferen der Plankton Expedition,' Part I, pp. 228-229, fig. 41, and Plate 39, fig. 27 (Kiel, 1909).)

² A. HANCOCK, "On the Excavating Powers of Sponges, with Descriptions of New Species" ('Ann. Mag. Nat. Hist.,' Ser. 2, vol. 3, pp. 330-332, Plate 13, figs. 3, 4). It must, however, be borne in mind that the methods employed in *Cliona* in boring its tunnels are at present entirely obscure, though a comparatively extensive literature has gathered around it (cf., *inter alia*, E. TOPSENT, "Sur le Mécanisme de la Perforation des Cliones," 'Arch. Zool. Expérimentale et Générale,' 1894, pp. 10-13); and Prof. DENDY is of opinion that the tunnels are bored, or rather dissolved out, by chemical action.

In any case I think it will be without difficulty admitted that the discovery of these encrypted *Cymbaloporæ* throws a new and striking light upon the processes by which the calcareous *Monothalamia* enlarge their shells, and it is to be hoped that further material from these localities sent home preserved, whilst quite fresh and living (in Maier's or Schaudinn's fluids), may throw further light upon the subject.

VIII. ON THE DIFFERENT MODES OF SECRETION, GROWTH, AND REGENERATION OF THE CALCAREOUS SHELL OF THE FORAMINIFERA.

That the mechanical activities of the Foraminifera exhibit an amazing development in the direction of *purpose* is obvious to the most superficial observer of the exquisite calcareous tests secreted by the hyaline and porcellaneous Foraminifera. How much the more so must it be to those who have made any extended researches in connection with the highly "intelligent"—I use this word advisedly and with full knowledge of the criticism which I invite in using it—the highly "intelligent" methods exercised by those Foraminifera which build their shells out of fortuitous materials, and which are classed in the two groups *Astrorhizidæ* and *Lituolidæ*? In the former group, the calcareous-shelled Foraminifera, it is difficult, if not impossible, to make the remotest guess at what influences the organism in secreting its marvellous investment as presented in its most elaborate forms.¹ As GAMBLE has said, in dealing with the Radiolaria, "So complex and diverse a tracery seems utterly beyond the needs of simple Protozoa living under apparently similar conditions of pelagic life; and though attempts have been made to explain this manifold skeletal development in terms of cytoplasmic structure, its variety still evades biological treatment," and he expresses the hope that as we come to regard the skeleton as a response to the varying media, stresses, and strains that fall upon the cytoplasm from within or from without, its utilitarian character will be more completely recognised.² Speculation is paralysed when one is confronted with the fact that of two groups of the same zoological order, composed of the same simple protoplasmic element and living under precisely similar conditions, one group should secrete from an identical environment for the purpose of constructing its shell calcium carbonate, whilst the other constructs its test of strontium sulphate.³ As DENDY has pregnantly observed, "The fact that one organism will select silica, whilst another selects carbonate of lime from the same sample of sea-water and for

¹ A scholarly discussion upon, and an attempt to solve, these problems is afforded by F. DREYER in two elaborate articles, the first in the 'Biologisches Centralblatt' (vol. 9, p. 333 (1889)), and the second in the 'Jenaische Zeitschrift für Naturwiss.,' 1892 (p. 219), to which the student is referred. Abstracts of these papers were published in the 'J. R. Micr. Soc.,' p. 768 (1889); p. 767 (1892).

² F. W. GAMBLE, "Radiolaria," in L. 1909, T.Z., vol. I, pp. 130, 131 (1909).

³ O. BÜTSCHLI, "Ueber die chemische Natur der Skelet-substanze der Acantharia," 'Zool. Anzeiger,' Leipzig, pp. 784-789 (1909).

the same purpose, must correspond to some deep-seated difference in the protoplasm of which they are composed, and illustrates very well the diverse potentialities of this remarkable substance."¹

But we do know that the substance and the design of the shells of the calcareous Foraminifera can be artificially influenced and modified when the organisms are kept and cultivated in captivity. It is a matter of common observation that the shells of Foraminifera which have been cultivated through a long series of generations in micro-aquaria have a tendency to become excessively hyaline and transparent, and even to become chitinous instead of calcareous, if the salinity in the tanks is maintained at a fixed rate by the addition of *distilled* water to counteract evaporation. SCHAUDINN attributes the ease with which he was enabled to observe the nucleus in living *Patellina corrugata* partly to this cause,² and there is little doubt in my mind that some such factor as this accounted for SCHULZE's highly transparent species *Spiroloculina hyalina*.³ On the other hand in a tank in which I cultivated many generations of *Massilina secans* (d'Orbigny) in my laboratory at Selsey, in which the salinity was kept at a fixed standard by the addition of *tap* water (from my own wells) which was markedly hard owing to the presence of lime, some interesting and extraordinary modifications of the shells were brought about. In this case, far from the shells becoming weak and hyaline, they had a tendency to add striæ and ridges of secondary shell-substance upon the surface of the shell, and marked carinations and denticulations round its periphery, so much so that though the original parents in March, 1910, were nothing but *Massilina secans* (d'Orbigny), in October of the same year the tank was inhabited by quite remarkable quantities, not only of the original species, but also of the very marked varieties *denticulata* (Costa),⁴ *tenuistriata* (Earland),⁵ and *obliquistriata* (Halkyard)⁶ (fig. 57). It was also observed that the Miliolinæ grown in this tank showed a marked activity and response to disturbance, in the direction of repairing damage to their shells. Nothing is, unfortunately, easier, when picking out a living Miliolid from the tank for observation, than to smash it. These smashed specimens were always put back into the tank immediately, and as a result, when the bottom-mud was finally washed out and examined, the number of monstrous specimens in which this damage had been repaired by the extrusion of

¹ D. 1912, E.B., p. 26.

² "In einzelnen Gläsern waren die Schalen der Patellinen so kalkarm und daher durchsichtig, dass man die Kerne gut erkennen konnte; dies dürfte daher rühren, dass in diesen Gläsern mehrere Jahre hindurch viele Generationen von Foraminiferen gezüchtet waren und infolge dessen im Meerwasser nicht mehr Kalk vorhanden war." S. 1895, P.F., p. 182.

³ S. 1874, etc., R., No. 3, 1875, p. 132, Plate VI, figs. 14-16.

⁴ *Quinqueloculina denticulata*, O. G. COSTA, 1856, 'Atti Acad. Pontaniana (Naples),' vol. 7, fasc. 2, p. 325, Plate 25, fig. 6.

⁵ E. 1905, F.B.S., p. 198, Plate 11, fig. 5.

⁶ *Sigmoilina secans* var. *obliquistriata*, E. HALKYARD, 1889, "Recent Foraminifera of Jersey," 'Trans. and Ann. Rep. Manchester Micr. Soc.,' p. 63, Plate 1, fig. 7 (1889).

protoplasm and the formation of eccentric and wild-growing supplemental chambers was extraordinarily large¹ (fig. 58).

I have here neither the time nor the space to go into the highly interesting question of how the monothalamous calcareous Foraminifera of the group *Lagena* increase the size of their shells. The study of the life-history of this group is rendered so difficult that it almost may be described as impossible by the fact that there is no primordial chamber to be studied, or rather that the whole adult test is itself an expanded primordial chamber. The youngest specimens found present no difference of characteristics from the adult, but I think there can be no doubt that the same power that enables the animal to secrete the carbonate of lime forming its shell enables it at any given moment partially to redissolve it, and to add newly secreted material for the enlargement of the shell by a process of intussusception. The theory that the monothalamous Foraminifera *periodically* cast their shells and build larger ones may be dismissed as fantastic,² but, as LISTER has acutely observed, "the student of the growth of bone will find no *a priori* difficulty in admitting that a rigid structure may be the seat of profound interstitial changes of substance."³

A highly notable illustration of this quality is to be found in the rare and exquisite species, *Carterina spiculotesta* (Carter), the shell of which is composed of blunted or highly fusiform spicules of carbonate of lime, secreted by the animal itself, and felted together on an extraordinarily co-ordinated plan, the spicules following the contour of the chamberlets on the upper surface, whilst at the base of the test they turn inwards so as to give the appearance that they radiate from the centre (fig. 59). The growth and development of this organism is sufficiently interesting to form the subject of a monograph by itself, to which on some future occasion I hope to be able to address myself.⁴ All that is necessary to be pointed out at the present is that the growth of this shell is apparently effected by the simultaneous expansion of every spicule in the shell, and the intercalary addition of new ones which make their first appearance as tiny globular bodies, the whole being welded together by an interstitial cement of the same character as the spicules themselves.⁵ A comparison may be instituted between *Carterina spiculotesta* and *Euglypha alveolata*, whose test is

¹ See H-A. and E. 1908, etc., S.B. 1910. "A Contribution towards the *Ætiology* of *Massilina secans* (d'Orbigny), p. 695.

² This theory was seriously advanced by ALCOCK in his "Questions regarding the Life-history of the Foraminifera, suggested by Examinations of their Dead Shells," 'Proc. Lit. and Phil. Soc. Manchester,' vol. 5, p. 17 (1866), in which he suggested that the monothalamous Foraminifera took advantage of these moments when they were changing houses to multiply by fission.

³ L. 1903, F., p. 55.

⁴ See H. J. CARTER, "Description of a New Species of Foraminifera, *Rotalia spiculotesta*," 'Ann. and Mag. Nat. Hist.,' Ser. 4, vol. 20, p. 470, Plate 16 (1877); Ser. 5, vol. 3, p. 414 (1879); and Ser. 5, vol. 5, p. 452 (1880).

⁵ See our Kerimba Monograph, 'Trans. Zool. Soc.' (1915). (*In the press.*)

formed of siliceous or chitinous plates secreted in the substance of the protoplasm near the nucleus, whence they pass to the surface to be built together into a regular test.¹ A similar secretion of spicules, but in this case siliceous, is stated by VON DADAY to take place in his species *Entzia tetrastomella*,² which, however, I have never had an opportunity of seeing; nor have I ever seen any Foraminifera suggesting the Miliolids from great depths (3950 fathoms, BRADY), stated to bear a siliceous shell, which were recorded by BRADY, and upon his authority are referred to in more than one work on the Foraminifera,³ nor the *Polymorphina silicea* of MAX SCHULTZE.⁴ Without an inspection of the original material it is perhaps rash to make any authoritative pronouncement, but it has always seemed to me more than probable that these so-called siliceous Foraminifera were really formed of an especially tough chitin, as might be expected at great depths where carbonate of lime becomes broken down, and it is possible that their observers (if any there be, besides Sir JOHN MURRAY, which is by no means clear to my mind) may have been misled by the known resistance of these chitinous shells to acid or alkaline reagents. I think, however, that the matter is considerably clarified, if not settled, by the extracts from Sir JOHN MURRAY's Journal, cited by his permission in Appendix B.⁵

Before leaving this question of the secretion and growth of the calcareous tests I may be allowed to call attention to a very interesting section (fig. 60) of a fine specimen of *Vaginulina linearis* (Montagu) in which the addition of the successive

¹ M. 1912, I.S.P., pp. 111-113, fig. 59.

² E. VON DADAY, "On a Polythalamian from the Saltpools near Déva in Transylvania" (translated from 'Zeitsch. f. Wiss. Zool.', vol. 40, pp. 465-480, by W. S. DALLAS), 'Ann. and Mag. Nat. Hist.', Ser. 5, vol. 14, pp. 349-363 (1884).

³ B. 1884, F.C., p. 131; L. 1903, F., p. 53, etc. The evidence for the occurrence of these "siliceous" Foraminifera rests, like that for the "monadiform bodies" from *Cymbalopora bulloides*, upon a paragraph of BRADY (here cited). BRADY's paragraph is misleading. His only source of information lay in the slides prepared by Sir JOHN MURRAY on board the "Challenger," and Sir JOHN MURRAY's notes, which he has permitted me to transcribe from his laboratory note-books kept on the cruise, do not justify this assumption and diagnosis (see Appendix B). It is unfortunate that Dr. BRADY did not consult Sir JOHN MURRAY's note-books carefully before publishing his paragraph, and a matter for regret that Sir JOHN MURRAY's note-books have never been published, excepting in so far as he has transcribed them in the two volumes of 'Summary of Results' (1895). There is nothing in his observations inconsistent with the presumption that these so-called "siliceous" forms were the chitinous remains of calcareous Foraminifera, after treatment with acid, but rather on the contrary. BRADY's paragraph conveys the impression that he himself observed these siliceous Miliolids, but Sir JOHN MURRAY informed me that the observations were made by him in open stage-cells on board the "Challenger," and that the specimens were not preserved.

⁴ This species recorded by SCHULTZE (S. 1854, O.P., p. 61, Plate 6, figs. 10, 11) is generally adopted as a synonym of *Verneuilina polystropha* (Reuss). (B. 1884, F.C., p. 386.) SCHULTZE was of opinion that the siliceous plates forming the test of this species were secreted by and within the protoplasm of the organism, and incorporated with the substance of the shell as required. (Cf. VON DADAY, *loc. cit.*, Note 161, p. 355.)

⁵ As to the nature of chitin see C. 1901, P., pp. 39, 40.

layers of shell matter laid down on the outside of the shell by the extruded protoplasm is very clearly marked, exhibiting a construction-process, doubtless universally adopted, which has been admirably figured and described by BEISSEL.¹

IX. ON SELECTION AND GROWTH IN SOME ARENACEOUS FORAMINIFERA.

When we arrive at the consideration of the arenaceous forms it behoves us to proceed with the greatest possible caution, for the phenomena exhibited reveal an apparent development of purpose, and what in the Metazoa would be termed "intelligence," which is apt to lead the imagination very far astray unless it is kept rigidly within the bounds imposed by the observed results, from which results it is, in dealing with these organisms, most especially dangerous to generalise. This is a danger from which it would appear some of the authors cited in this paper have not wholly escaped.

In spite of the many ingenious theories that have been put forward, the method in which the mud, the sand, the shell-detritus, the sponge-spicules, the echinoderm-debris, and even the shells of smaller species, are collected by the animal and formed into a test, always of more or less marked ingenuity, and sometimes of amazing beauty, remains to a great extent obscure.² The matter was gone into at great length by myself and EARLAND in our address before the British Association in 1912,³ in answer to Dr. LUDWIG RHUMBLER's elaborate theory of the multiform life-cycle of *Saccammina sphaerica*, M. Sars,⁴ the three stages of which we identified as being respectively *Crithionina mamilla*, Goës,⁵ which represents his primordial chambers (*Primitiv-Gehäuse*), *Psammosphæra fusca*, Schulze,⁶ which represents his young form (*Jugendstadium*), and the adult and perfect *Saccammina sphaerica*, M. Sars.⁷ For reasons which we there set out at length, we find it impossible to accept RHUMBLER's theory that the organism extrudes protoplasmic processes from various parts of the shell upon which it collects sand particles with a view to enlarging that particular portion of its test, these fistulose sand-invested processes being commonly found upon the exterior of the shell in dredgings rich in

¹ B. 1891, A.K. Atlas, Plate 2, figs. 6-10.

² For a general sketch of this subject I may refer the student to Canon NORMAN's highly suggestive and interesting paper "On the Architectural Achievements of Little Masons, Annelidian (?) and Rhizopodan, in the Abyss of the Atlantic," 'Ann. Mag. Nat. Hist.,' Ser. 5, vol. 1, p. 284 (1878).

³ H-A. and E. 1913, S.P. See also Abstract in 'Report, 82nd Brit. Ass. Meeting, Dundee, 1912,' London, 1913, pp. 498-99.

⁴ R. 1894, S.S. In this paper RHUMBLER sought to identify two very distinctive forms as stages in the life-cycle of *Saccammina sphaerica*. His views were to some extent supported by FRITZ LUCKE (L. 1910, S.S.) and were further discussed at great length by E. HIRSCH (H. 1912, E.S.), but in our opinion the original postulate was at fault, owing to insufficiency of the material subjected to examination.

⁵ G. 1894, A.S.F., pp. 13-14, Plate 3, figs. 16-19.

⁶ S. 1874, N.R., p. 113, Plate 2, fig. 8.

⁷ S. 1871, H.F., p. 250.

Saccamina, and representing damaged individuals, which are attempting to make good the damage in the manner common among the calcareous-shelled species to which reference has already been made (*vide ante*, p. 262). Our views were, in our opinion, confirmed by the discovery, in all dredgings where Saccamina is abundant, of specimens so loosely coherent and fragile that they break into fragments at a touch. Now, Saccamina is normally a very robust form (fig. 61), extremely difficult to crush or to break open with a needle, and we are justified in concluding that these friable specimens are individuals which have been caught in the dredge just at the moment when the animal has re-dissolved the cement with which its "house" is built, with a view to increasing its size by the interstitial addition *from within* of stored material.¹

What guides the animal in the choice of its material appears to be beyond the reach of all hitherto elaborated methods of research, though it clearly appears that the process may be artificially induced and guided. For instance, MAX VERWORN was able to compel *Diffugia* to build its test out of various materials (such as particles of coloured glass or other substances) when these were supplied to it, to the exclusion of other material.² I can see no necessity for seeking further than the observations of VERWORN to account for the manner in which the arenaceous monothalamia increase the size of their shells. It is not, as in the case of the calcareous monothalamia, an intercalary (or interstitial) *growth* of shell substance by intussusception, but an intercalary *deposit* or placing of grains collected within the test by the retractile processes of the pseudopodia, and utilised when the need of a larger "house" arises from the development of the protoplasmic body.³

An experiment similar to that of VERWORN is at this moment in course of development in connection with the species *Haplophragmium agglutinans* (d'Orbigny) in my tanks at Selsey. The species is extraordinarily abundant, and reaches magnificent proportions among the algæ growing upon the loosely aggregated

¹ The difficulty in studying the life-history of the calcareous monothalamia to which I have adverted (*supra*, p. 263) is encountered in an aggravated form in the case of the arenaceous monothalamia, the rapid expansion of the test obliterating any indication of the size of the youngest stage of the test, and of course *a fortiori* rendering any speculations as to dimorphism in these forms entirely futile. (Cf. L. 1903, F., p. 78.)

² V. 1888, B.P.S. and M., 1912, I.S.P., pp. 34-36. VERWORN observed that the foreign particles are taken up by the pseudopodia during the process of being retracted; the surface of the pseudopodium then becomes wrinkled, and particles of *débris* are caught in these wrinkles, and so drawn into the interior of the protoplasmic body, in which they are stored up in the fundus of the shell (like the plates in *Euglypha*) and are utilised in the growth of the shell, or in repairing damages to it, or in building a new shell when the animal reproduces itself by division.

³ "There can be little doubt that *Diffugia* exercises a deliberate choice of the particles it uses for shell purposes, and to a certain extent the character of the foreign particles and their arrangement can be used for racial or specific distinctions." HICKSON, Art. "Lobosa" in L. 1909, T.Z., p. 85.

rocks of the Mixon Beacon, some two miles out at sea from the point of Selsey Bill (fig. 62).

The sands found in the rock pools at this locality (a ground which, it may be remarked, is not harassed or complicated by any system of local drainage, or by any immediately neighbouring river outflow) contain an infinitely small proportion of garnet, magnetite, and a yellow gem which I take to be topaz. One of the commonest Foraminifera of the locality is *Verneuilina polystropha* (Reuss) and among the shells of this species, the majority of which are neatly constructed in the ordinary way, of very small quartz grains, built together with a brilliantly white, or deeply ferruginous cement (which gives a very distinctive colouring to the shells), frequent specimens are found (fig. 63) which have selected and built into their shells relatively large fragments of these gem materials, and though even I would shrink from suggesting the inclusion among the higher qualities of Foraminiferal protoplasm of an "æsthetic sense," the selection of these grains of markedly higher specific gravity by a *very restricted proportion* of the animals of this species seems to me to be exceedingly significant. It affords a parallel to the instances of selection, by different species living on the same bottom, and surrounded by the same materials, of entirely different elements, to which LISTER has called attention.¹

The "intelligence" which, I am bold enough to claim, is displayed by the arenaceous Foraminifera in their house-building takes two forms: first, the exclusive selection of certain materials, and second, the manner in which they are used. The highest exhibition of the former phenomenon is to be found in the species *Technitella thompsoni*, discovered by us among dredgings made by the Fisheries cruiser "Goldseeker" in the North Sea. The genus *Technitella*, to which Canon NORMAN first called attention in the year 1878, builds its shell normally, as described by Canon NORMAN, "of the fragments of minute acerate spicula, laid in regular order side by side, and cemented with a mortar composed probably of the finest dust of quartz, so that the whole test is of exquisite snowy whiteness." The accidental destruction of a specimen of *Technitella legumen*, Norman, however, revealed to us the astonishing fact that the whole shell wall consists of two distinct layers of spicules, an outer layer in which the spicules are all laid with their long axes parallel to the long axis of the test, and an inner layer of spicules laid with their long axes at right angles to the outer layer, giving as close an approximation to the woof and warp of a textile fabric as is possible with a rigid non-flexile material such as sponge-spicules. It is obvious that by the crossing of these two layers the

¹ L. 1903, F., p. 52. Fig. 64 represents two specimens of *Reophax difflugiformis*, Brady, exhibiting the same selective tendency. It must be particularly borne in mind that the quartz-grains of which these species normally build their shells have a specific gravity of 2.65, whilst the specific gravity of the incorporated gem-particles is much higher (*e.g.* garnet, 3.7-4.1). Anyone who has tried to mix the two in an aquarium will have observed that the heavier gems *invariably sink*, so that they are not to be found upon the surface-layers of the sand where *Verneuilina* and *Reophax* live and construct their tests.

strength and resistance of the test to strain is enormously increased. It is, however, interesting to note that *Technitella legumen* seldom employs broken spicules, thus securing material of practically standard size.¹

But in the same series of dredgings that contained *Technitella legumen* we have found a species (which we named after Prof. D'ARCY THOMPSON) which selects from the abundance of other material at its command nothing but a particular local type of echinoderm plate, which plates, when utilised by the organism, overlap each other and are fastened together without visible cement. The organism has no definite oral aperture, the foramina for the extrusion of its pseudopodia being afforded by the perforations of the echinoderm plates, thus making the animal one of the most highly perforated Foraminifera in existence.²

Another instance of the astonishing design and "intelligence" displayed by the Foraminifera in the use of sponge-spicules is to be found in the species *Psammosphæra rustica*, Heron-Allen and Earland, first dredged by EARLAND on the "Goldseeker" in the North Sea. This creature, living on extremely muddy bottoms, uses long sponge-spicules, often 2 and 3 mm. in length, in a manner which can only be compared to tent poles. They are placed at various angles about 0.5 mm. apart, forming a rough openwork figure enclosing a central space between the points of intersection of the poles. The open spaces in the wall are then filled in with fragments of spicules carefully selected for length so as exactly to fill the spaces that are to form the walls of the test, an awkward triangular terminal space being frequently filled in with a truncated triaxial spicule. The nearest possible approach is thus obtained to a spherical chamber, regard being had to the material employed. The animal inhabits this quasi-spherical chamber (which, in common with the other species of the genus *Psammosphæra*, has no definite aperture), and the projecting ends of the longer spicules serve it as "catamaran spars" in supporting the animal on the surface layer of the ooze. At times when the long spicules are longer than usual, a second and often a third individual will make use of the extreme ends and build a similar house. A pair or series of three connected in this way by their "catamaran spars" are entirely distinct organisms, their only connection with one another being a purely utilitarian one, the association offering greater resistance to the mud than a single individual can attain. The pseudopodia of this co-operative society must necessarily intermingle, but we have not been able to keep the animals alive so as to observe

¹ See H-A. and E. 1912, N.A., pp. 382-389, where these phenomena are fully figured.

² H-A. and E. "On a new species of *Technitella* from the North Sea, with some Observations on Selective Power as Exercised by Certain Species of Arenaceous Foraminifera," 'J. Quekett Micr. Club,' Ser. 2, vol. 10, pp. 403-412. It would have been remarkable if this tendency to a highly specialised selection had escaped the daily observations of so keen an observer as the late Sir JOHN MURRAY. At p. 511 of his great work 'Summary of Scientific Results of the Voyage of H.M.S. Challenger' (London, 1895), we find him noting specimens of *Astrorhiza crassatina*, Brady, forming its test almost exclusively of the spherical Radiolarian *Cromyosphaera antarctica*; and of *Reophax nodulosa*, Brady, using large Coscinodisci, arranging them flatwise over the surface, and so on.

whether their pseudopodia anastomose with one another or not. But we have here an unanswerable argument in support of the supposition that these highly organised Protozoa are endowed with what might be termed a "social instinct" for their mutual assistance and protection, apart from the remarkable technical skill which they display in constructing their individual houses.¹

A further and perhaps even more striking display of "intelligence" is that exhibited by another species found by us in the same dredgings, *Marsipella spiralis*, Heron-Allen and Earland. The previously known *Marsipella cylindrica*, Brady, forms a long and very friable tube, selecting for the purpose broken sponge-spicules of approximately equal length (in contrast to *Technitella legumen*, which seldom or never employs a broken spicule). Its test is exceedingly friable, and it would appear that, a long series of generations of *Marsipella cylindrica* having suffered from this extreme friability, it was left for *Marsipella spiralis* to make the same great discovery as did the prehistoric genius who invented string—it has clearly realised that a twisted yarn is stronger than an untwisted wisp of fibre. The spicules of *Marsipella spiralis* are always arranged in a left-handed spiral, firmly embedded in a cement similar to that employed by *Technitella*.²

In *Marsipella cylindrica* we have been able to establish the fact, by the finding of perfect specimens (which BRADY was unfortunately not able to discover) that the apertural end of the organism consists of a club-shaped head, often two or three times the diameter of the tube, and composed of loosely aggregated sponge-spicules from which a number of longer spicules (from 0.5 to 0.8 mm.) radiate in all directions, thus forming an effective *chevaux de frise* which must prove a very efficient protection against the attacks of parasitic worms, a phenomenon which is exhibited also by *Haliphysema tumanowiczii*, Bowerbank, and *Hyperammina ramosa*, Brady, in which species the entire body of the animal is protected in a similar manner.

That the arenaceous Foraminifera are not always guided in the construction of their tests by considerations of strength and resistance, however, is proved by the exquisite species *Reophaex scottii*, Chaster (fig. 65), which builds an extremely fragile polythalamous tube out of infinitesimally small flakes of mica, joined at their extreme margins by chitinous material. This test when alive, or when

¹ H-A. and E. 1912, N.A., pp. 383-385. This highly significant use of a long sponge-spicule as a "catamaran spar" is also made by a species of *Psammosphæra*, *P. parva*, Flint (F. 1899, F.A., p. 268, Plate 9, fig. 1, and H-A. and E. 1913, S.P., pp. 17-18, Plate 2, fig. 8), which builds its test round a long spicule which projects on opposite sides of the spherical test, sometimes to a length many times exceeding the total diameter of the test. The species was also figured, but without comment, by BRADY (B. 1884, F.C., Plate 18, fig. 4). It is of very rare occurrence, but of very distinctive form and construction as compared with the normal *Psammosphæra fusca*, and there can be but little doubt that the animal deliberately chooses the spicule as a main constituent of its house, in order to obtain the increased support afforded by its projections in supporting itself upon the surface layers of the bottom ooze.

² H-A. and E. 1912, N.A., pp. 387-8.

wetted after drying, is quite pliable, and so delicate as practically to defy manipulation.¹

X. CONCLUSION.

In the foregoing pages I have attempted to record as shortly as possible observations, both old and new, of phenomena which, I venture to say, afford proofs of the correctness of the view upon which I have founded this paper, namely, that the Foraminifera exhibit the highest functions and the most "intelligent behaviour" of which undifferentiated protoplasm has been observed to be capable. Whether the hope of CLAPARÈDE and LACHMANN, "that the sarcode of the Rhizopoda may some day find its chromic acid," is destined to be realised, is a matter for later and very assiduous investigation, an investigation in which bio-chemistry must necessarily play an important part.

I venture to predict that the recent investigations and experiments of BARNARD, upon which I have elsewhere expressed views which, in the opinion of some zoologists, are Utopian,² are opening up a new method of biological research, the bearings of which upon the solution of hitherto insoluble problems in the nature of protoplasm and the life-histories of the Protozoa can hardly be overestimated.

But apart from such profound studies as these, I may perhaps be permitted to express the fervent hope (whilst in no way belittling the labours of pure systematists) that students of the reticularian Sarcodina will devote themselves to the elucidation of these questions, rather than to the identification and multiplication of species.

The unicellular organisms, as VERWORN has truly observed, seem to have been created by nature for the physiologists, for, besides their great capacity for resistance, of all living things they have the invaluable advantage of standing nearest to the first and simplest forms of life.³ And of all the unicellular organisms, the Foraminifera appear to me to lend themselves most readily to biological investigation. The relatively gigantic proportions of their protoplasmic bodies, the readiness with which they may be collected, and the ease with which they can be kept alive, watched, and bred in captivity, all combine to single out the group for the earnest attention of the biologist.

Not only are the magnificently appointed Marine Biological Laboratories such as those at Plymouth, Port Erin, and Millport, ever ready to welcome students and place their infinite resources at the service of the investigator, but nothing is easier than to maintain in healthy and prosperous condition a series of small observation tanks in the heart of great inland cities. I have myself kept such tanks in London for many years, and the living Foraminifera have one supremely valuable quality—

¹ C. 1892, F.S., p. 57, Plate 1, fig. 1.

² See J. E. BARNARD, "X-rays in Relation to Microscopy," 'J. R. Micr. Soc.,' 1915, p. 1, and 'Proceedings of the Society,' *Ibid.*, p. 87, and HERON-ALLEN, 'Proc. Zool. Soc. (Lond.),' 1915, p. 152.

³ C. 1901, P. p. 2.

that they do not resist or suffer from occasional, unavoidable neglect. I may be unduly prejudiced, but it seems to me that there is no branch of zoological enquiry more attractive to the student, not only by reason of the remarkable interest and beauty of the creatures themselves, but by reason of the close proximity to the origin of life, into which we are brought by patient observation of their readily studied life-histories.

APPENDIX A.

Cymbalopora bulloides.

(Extracted from Sir JOHN MURRAY'S laboratory note-books kept on board H.M.S. "Challenger.")

(*The words in italics are mine and do not appear in the Journal.*)

July 27, 1875.—*In the Harbour of Honolulu.* In the tow-net this morning there were large numbers of Foraminifera we have not hitherto noticed on the surface. (*Follows, a careful description of Cymbalopora bulloides, accompanied by detailed drawings, showing the internal "float-chamber" distinctly.*) These were all got on the surface, very few being got in a deeper haul than the surface. All of them had a bubble of air in them (*i.e. in the float-chamber*), which was difficult to expel in mounting. There was some yellow matter in them, but apparently not active. All of them—for I examined very many—had in them immense swarms of very minute organisms, which burst forth and swam about on the shell being crushed. At first I imagined these Foraminifera were in a state of decay and that the small bodies were bacteria, but, after examination with the highest powers, I think there is reason to doubt this.

With my highest combination (10×4)¹ the bodies appear all the same size, have a bluish refractive spot at one end, from which hangs a sort of bag to which I think there are some cilia. The organisms proceed across the field with a rapid rotating motion. The cilia are very difficult to observe well (*a drawing, which I reproduce, is here inserted*). These little bodies colour with carmine at one end.

These Foraminifera are not all the same size. Some are very much smaller than the others, but the same in other respects.

July 28, 1875.—Remained on board this forenoon and examined some of the Foraminifera taken yesterday. Those in a globe still had the small swarms still alive. Some in a glass had no motion—seemed dead—but there were about them no signs of decay as yet.

August 4, 1875.—In the surface net were the usual surface things, and the new Foraminifera, still the monad-like creatures, were very abundant.

August 11, 1875.—(*Outside the Harbour of Honolulu. Referring to the dredging operations on the 4th.*) The Foraminifer (*C. bulloides*) was abundant all the while we were in harbour. I never found them without the small active organisms, and I was not able to detect any change in these.

August 20, 1875.—(*Some C. bulloides recorded as present in the tow-net.*)

September 6, 1875.—(*After sounding in 2425 fathoms the tow-net was sent down with 200 fathoms of line.*) Some very large living Foraminifera in this haul. In one slide under the microscope I came across a great swarm of the same ciliated bodies that were continually in the Foraminifera taken while at Honolulu on the surface. Many of them were larger than I then saw (*a drawing, which I reproduce, is here inserted*). Could not tell whether they had been squeezed from a Globigerina or not.



July 27, 1875.



September 6, 1875.

¹ Objective, Hartnack No. 10 (water immersion); Ocular, Hartnack No. 4, J.M.

(On several other occasions Sir JOHN MURRAY records from his washings "*Amœba* or *amœboid* particles and also small ciliated bodies (? young of *Foraminifera*)"; cf. September 11 and 15, 1875, not associated with adult specimens. It has been suggested to me that these ciliated bodies were unicellular algae, but in the absence of the specimens this point cannot be determined.)

APPENDIX B.

Siliceous Foraminifera.

Sir JOHN MURRAY's notes are as follows:—

April 3, 1875.—Sounded in 4475 fathoms. "The lower portion (*of the sounding in the tube*) dried quite white on the slide and appeared as one mass of Radiolaria On one of these slides I found three Globigerina shells which had resisted the action of the acid. A drop of acid was placed on them, and after a moment they disappeared, leaving a slight skin, most likely of silica.

July 9, 1875.—Sounded in 3050 fathoms. I noticed not a single trace of any surface animal with carbonate of lime in its constitution—Globigerina or other. There were, however, three or four hyaline Foraminifera—like Triloculina. Separating these carefully and treating them with acid, I found that the complete form (not a membrane but a shell) remained after the action of the acid.

July 10, 1875.—Sounded in 2950 fathoms. I noticed one or two hyaline forms but the acid had no effect, and the same was the case with what I supposed was a large piece of Biloculina

[*Note.*—I see that in notes over a year ago I have noticed that sulphuric acid (weak) did not affect some of the Foraminifera shells in the deep soundings, but I had forgotten the circumstance. It now appears to me more likely that SO_3 is the agent concerned in the removal of the CaO.CO_2 from the shells than CO_2 , as supposed by THOMSON and BUCHANAN. This would account for more CO_2 in the bottom water and the presence of CaO.SO_3 in sea-water in such abundance. Also supported by the fact that in the South Polar Sea there is excess of SO_3 as well as in the lower water of the Mediterranean and Greenland currents.]

July 14, 1875.—Sounded in 3125 fathoms. I noticed one or two hyaline Foraminifera. These latter were affected only in colour by the acid. Their shell under the higher powers has much the appearance of the larger *Challengeria* I have frequently noticed remains of these in the soundings. They have a yellowish appearance and look mottled.

July 26, 1875.—Sounded in 2225 fathoms. One piece of a rather large Pulvinulina was the only trace of the surface Foraminifera noticed, and this, on treatment with weak sulphuric acid and afterwards with strong hydrochloric acid, did not all disappear. A film on the outside and inside of the shell seemed to be unaffected by the acid.

August 21, 1875.—Sounded in 2650 fathoms. I noticed one hyaline Foraminifer which did not effervesce with acid.

November 11, 1875.—(*After a description of a mass of "manganese nodules" from the tow-nets. The morning sounding had been in 1775 fathoms.*) Some of the larger ones had a yellow or dark green nucleus; this nucleus could be cut easily with the knife, like new cheese. Examined under the microscope, it presented many green and yellow specks having frequently agate bands, and Foraminifera could be easily seen embedded in the same mass. These Foraminifera were not, however, affected by acid. In some cases the external cast appeared only to be present, but in others the shell was still there, but all the carbonate of lime had been replaced by silica. Bird-claw-like extensions of the manganese ramified into this yellow nucleus, and it looked as if the manganese replacement was taking place towards the interior as well as manganese being deposited on the outside.

December 17, 1875.—Sounded in 1375 fathoms. After dissolving away a considerable quantity there remained a few red coloured casts of Foraminifera These lost their colour with strong hydrochloric acid.

March 9, 1876.—Sounded in 1700 fathoms. There were a good many more or less perfect casts of the Foraminifera in soft clayey matter. These usually broke up in the process of drying. In many of the chambers of these casts there were many particles of manganese, so much so as to colour some of these quite red or brown.

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EXPLANATION OF THE PLATES.

With the exception of figs. 37 and 38, which are from photographs, and fig. 45, which is after H. B. BRADY and Sir JOHN MURRAY, the drawings for these plates have been made from the specimens by Miss MABEL RHODES, Mrs. A. M. KING, F.R.M.S., and Mr. W. THORNTON SHIELLS.

PLATE 13.

- Fig. 1.—*Gromia dujardini* newly emerged from the mud on the floor of the aquarium. (From Selsey Bill.) $\times 60$.
- Fig. 2.—The same one hour later, climbing up the glass of the aquarium. $\times 60$.
- Fig. 3.—The same an hour later, having climbed up the stems of algæ. $\times 60$.
- Fig. 4.—The same an hour later, having moved from the alga stems to the glass of the aquarium. $\times 60$.

PLATE 14.

- Fig. 5.—*Miliolina durrandii*, Millett, containing an embryonic *Massilina secans*. $\times 75$.
- Fig. 6.—The same, a smaller specimen, containing two diatoms. (From the Kerimba Archipelago.) $\times 75$.
- Fig. 7.—*Massilina secans*, viewed by transmitted light after having ingested a hair, or cloth filament. $\times 40$.
- Fig. 8.—A similar specimen decalcified after ingestion of a hair. $\times 45$.
- Fig. 9.—A lost specimen of *Gromia*, attracted into the circle of light formed by a hole punched in black paper and illuminated. Its first appearance. $\times 60$.

- Fig. 10.—The same, after clearing away the weeds. $\times 60$.
 Fig. 11.—(a) Triple and (b) double “association” of individuals of the species *Discorbina globosa*, Sidebottom. (From the Kerimba Archipelago.) $\times 130$.
 Fig. 12.—*Discorbina mediterraneensis*, with contained young brood. (From Clare Island.) $\times 200$.
 Fig. 13.—*Discorbina wrightii*, with contained young brood. (From Bognor.) $\times 130$.
 Fig. 14.—*Discorbina parisiensis*, with contained young brood. (From West Scotland.) $\times 130$.
 Fig. 15.—*Planorbulina mediterraneensis*, with contained young brood. (From Bregançon Bay, Hyères.) $\times 75$.
 Fig. 16.—*Orbitolites complanata*, with young brood occupying the peripheral chambers. $\times 8$. From the Kerimba Archipelago.

PLATE 15.

- Fig. 17.—The same, fragments of partially resorbed shell-wall removed. $\times 12$.
 Fig. 18.—The same, embryonic young removed. $\times 24$.
 Fig. 19.—The same, part of fig. 16 more highly magnified. (From the Kerimba Archipelago.) $\times 12$.
 Fig. 20.—*Orbitolites complanata* with viviparous young. Section of edge viewed by transmitted light. (From the Kerimba Archipelago.) $\times 12$.
 Fig. 21.—*Lagena ornata* (Williamson) containing fully developed young shell. $\times 320$.
 Fig. 22.—Young (Adelosine) stage of *Miliolina agglutinans* (d'Orb.) with sand grains. (From the Kerimba Archipelago.) $\times 60$.
 Figs. 23 and 24.—Empty shells of *Discorbina parisiensis* after the escape of the young shells. (From Bognor.) $\times 130$.
 Fig. 25.—Glauconic cast of the protoplasmic bodies of an associated pair of *Discorbina pileolus* (d'Orbigny.) (From New Zealand.) Superior view. $\times 40$.
 Fig. 26.—The same—edge view. $\times 80$.
 Fig. 27.—*Discorbina parisiensis*, a-h, a series of “associated” pairs, the juvenile ranging from a single chamber to an adult shell. (From the Kerimba Archipelago.) $\times 100$.
 Fig. 28.—*Bulimina elegantissima*, a-f, a similar series. (From Delos.) $\times 100$.
 Fig. 29.—*Textularia agglutinans*, monstrous specimen in which a second and deformed shell has proceeded from (?) damage of the original test. (From Loch Sunart, West Scotland.) $\times 25$.
 Fig. 30.—*Bulimina elegans*, a double specimen. (From Loch Sunart, W. Scotland.) $\times 65$.
 Fig. 31.—*Hauerina compressa* (d'Orbigny), a specimen in which a litiiform (Peneropline) chamber has been added to the adult shell. (From the Kerimba Archipelago.) $\times 40$.

Fig. 32.—(a) *Lagena williamsoni* (Alcock), (b) *Lagena costata* (Williamson), (c) *Lagena squamosa* (Montagu), double specimens.

Fig. 33.—*Orbitolites complanata*, specimen with five primordial chambers. (From the Kerimba Archipelago.) $\times 12$.

PLATE 16.

Fig. 34.—Monstrous or multiform Foraminifer, combining the rotaline and nodosarine plans of growth. (From Loch Sunart, W. Scotland.) $\times 95$.

Fig. 35.—*Cymbalopora bulloides* (d'Orbigny). (a) Superior view; (b) inferior view; (c) side view; (d) small variety. $\times 65$.

Fig. 36.—*Cymbalopora milletti*, Heron-Allen and Earland. (a) Superior view; (b) side view. (From the Kerimba Archipelago.) $\times 65$.

Fig. 37.—*Cymbalopora*, shore gathering, Corny Point, Yorke Peninsula, S. Australia (MATTHEWS, 1880). $\times 12$.

Fig. 38.—*Cymbalopora*, pelagic specimens taken in the tow net, Honolulu Harbour (MURRAY, 1875). $\times 12$.

Fig. 39.—*Cymbalopora bulloides* (d'Orbigny), with abnormal or immature balloon-chambers. $\times 95$.

Fig. 40.—*Cymbalopora bulloides* (d'Orbigny), the entosolenian tube, terminating in spines. $\times 130$.

Figs. 41 and 42.—*Cymbalopora bulloides*, the balloon-chamber removed; and the float-chamber thus exposed, showing contained desiccated organisms, ? *Xanthellæ*. $\times 65$.

Fig. 43.—*Cymbalopora bulloides*, section showing balloon and float and entosolenian tube. $\times 65$.

PLATE 17.

Fig. 44.—*Cymbalopora bulloides*, with the float-chamber filled with ? *Xanthellæ*. By transmitted light. $\times 65$.

Fig. 45.—*Cymbalopora bulloides*, with the float-chamber indicated (after BRADY and MURRAY).

Fig. 46.—*Cymbalopora milletti*, showing the constrictions of the balloon-chamber. $\times 95$.

Fig. 47.—*Cymbalopora milletti*, after removal of the rotaline portion, showing the adherent walls of the "balloon" and "float," in three planes (diagrammatic): (i) broken terminal chamber; (ii) float-chamber adherent except at lobulations; (iii) the perforated base. $\times 130$.

Fig. 48.—*Cymbalopora milletti*, showing the "struts" formed by the lobulations of the float-chamber (side of terminal chamber removed). $\times 150$.

Fig. 49.—*Cymbalopora bulloides*, showing the rotaline aboral portion. $\times 130$.

Fig. 50.—*Cymbalopora milletti*, showing the acervuline aboral portion. $\times 130$.

Fig. 51.—*Cymbalopora milletti*, with (?) a rotaline embryo between the balloon- and float-chamber. $\times 130$ (slightly diagrammatic).

Fig. 54.—*Cymbalopora tabellæformis*, Brady, a colony encrypted in a molluscan fragment (nine crypts empty). $\times 15$.

PLATE 18.

Fig. 52.—*Cymbalopora poeyi*, d'Orbigny: (a) superior view; (b and c) inferior view; (d) section of high-domed specimen. $\times 65$.

Fig. 53.—*Cymbalopora tabellæformis*, Brady: (a) superior view; (b) inferior view; (c) side view. $\times 50$.

Fig. 55.—*Cymbalopora tabellæformis*, a specimen removed and set beside its crypt. $\times 50$.

Fig. 56.—A crypt of *Cymbalopora tabellæformis* from fig. 54, showing the radiating passages. $\times 50$.

(Figs. 35–56 are from the Kerimba Archipelago and Sir JOHN MURRAY'S Collection.)

Fig. 57.—(a) *Massilina secans* (d'Orbigny); (b) var. *denticulata* (Costa); (c) var. *tenuistriata* (Earland); (d) var. *obliquistriata* (Halkyard). Grown in captivity at Selsey. $\times 25$.

Fig. 58.—*Massilina secans*, monstrous specimen, caused by damage in the aquarium repaired by the animal. $\times 25$.

(Figs. 57 and 58 from Selsey. Bred in tanks.)

Fig. 59.—*Carterina spiculotesta* (Carter): (a) superior view; (b) inferior view. (From Torres Straits.) $\times 100$.

Fig. 60.—*Vaginulina linearis* (Montagu). Section showing the deposition of layers of carbonate of lime outside the shell. (From the North Sea.) $\times 65$.

Fig. 61.—*Saccammina sphaerica* (M. Sars). (From the North Sea). $\times 35$.

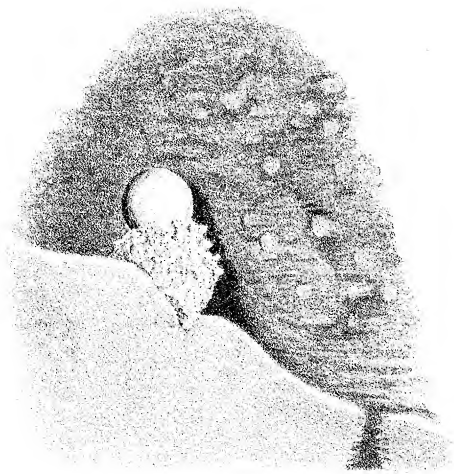
Figs. 62–64.—Arenaceous Foraminifera, showing the selection and incorporation of gem-fragments in the test.

Fig. 62.—*Haplophragmium agglutinans* (d'Orbigny). (From Selsey.) $\times 60$.

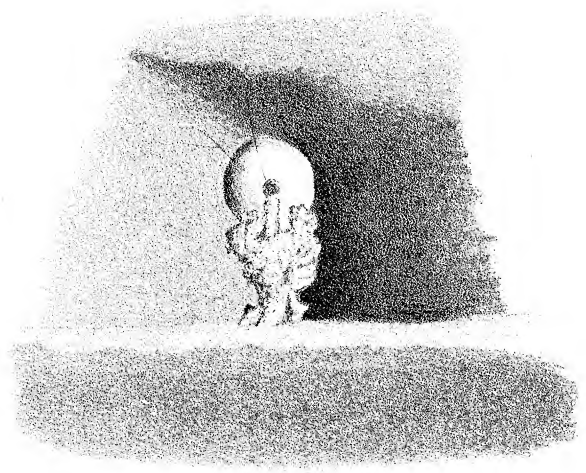
Fig. 63.—*Verneuilina polystropha* (Reuss). (From Selsey.) $\times 40$.

Fig. 64.—*Reophax difflugiiformis* (Brady). (From New Zealand.) $\times 40$.

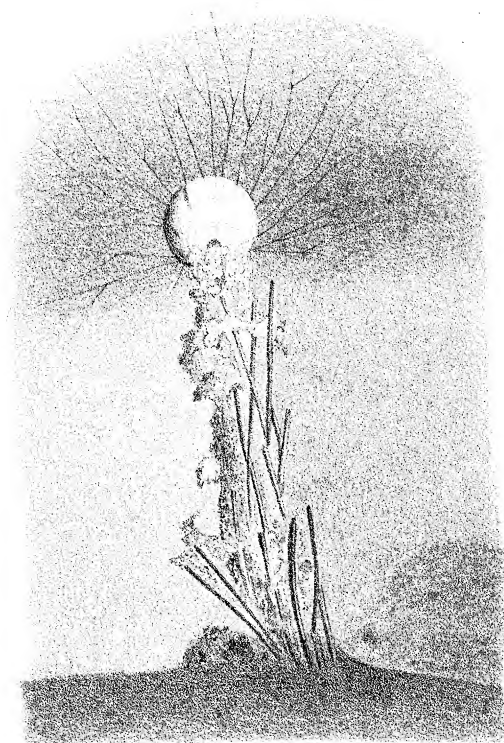
Fig. 65.—*Reophax scottii* (Chaster). (From the North Sea.) $\times 55$.



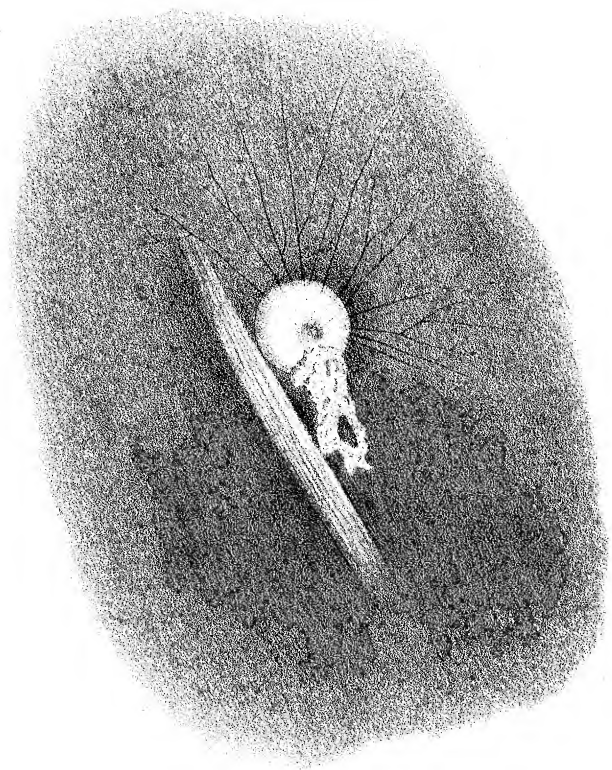
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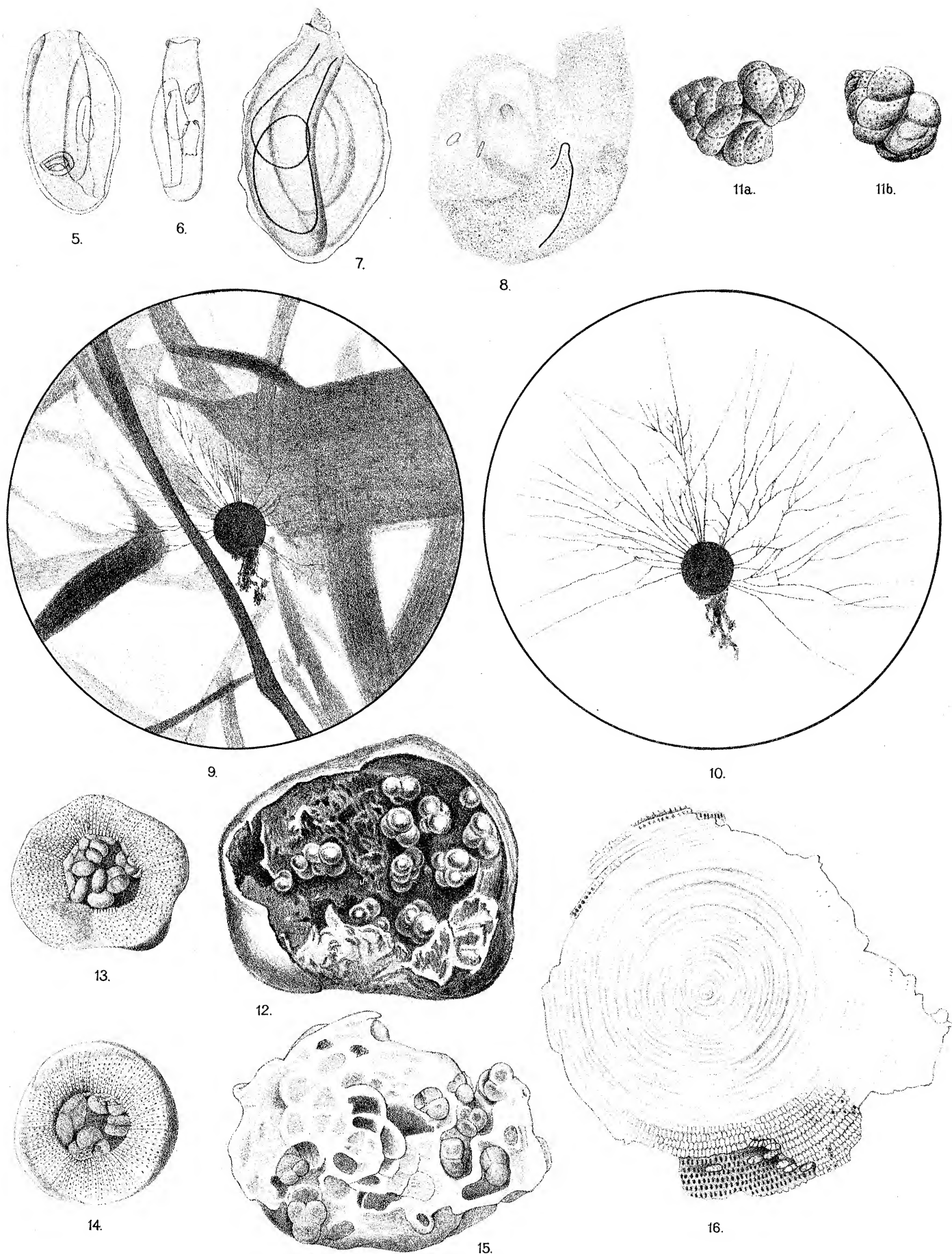
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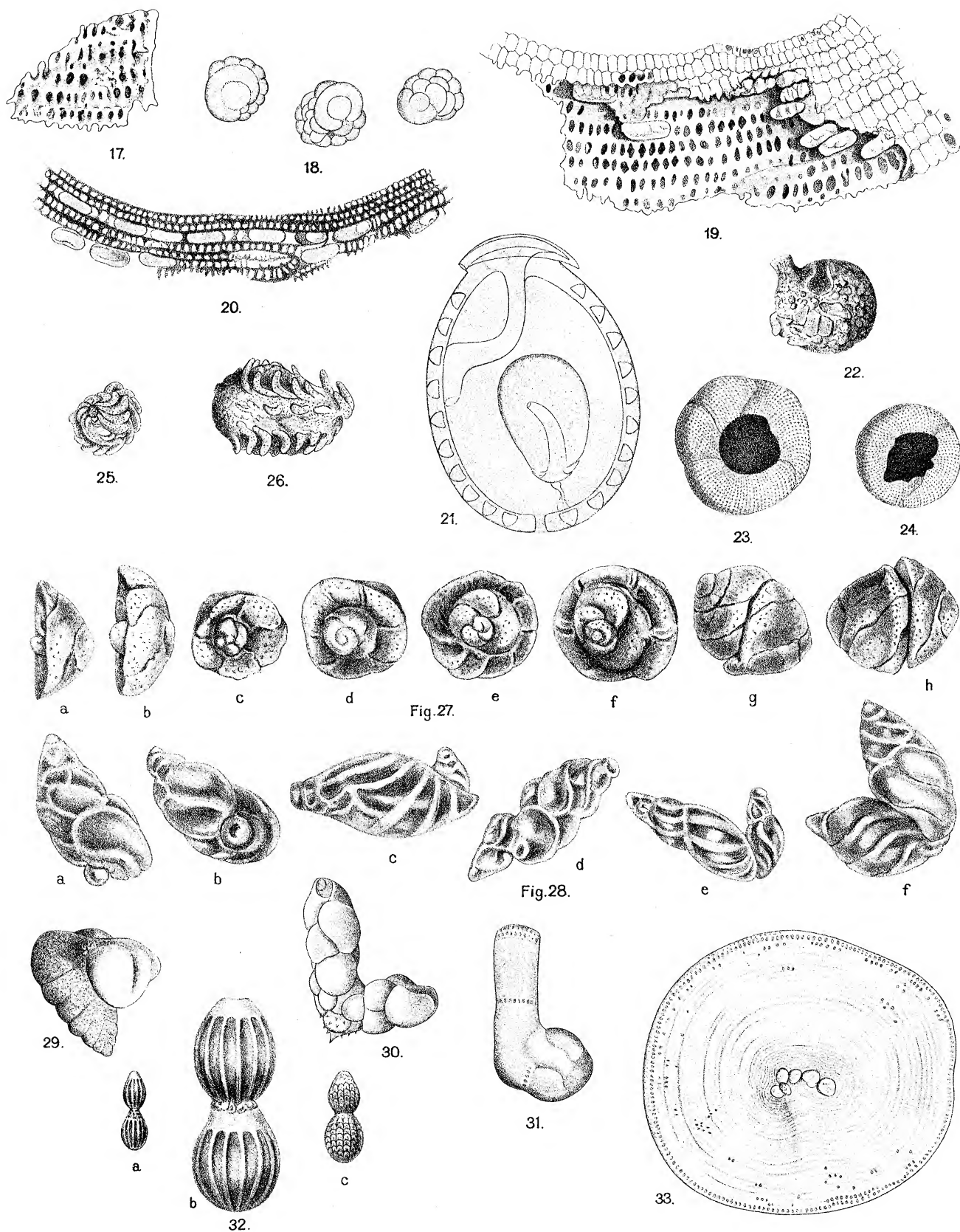


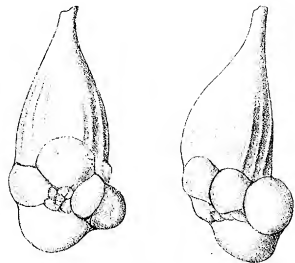
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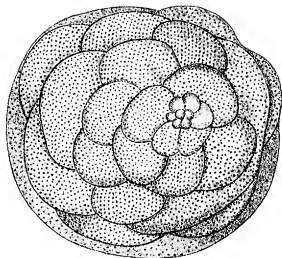
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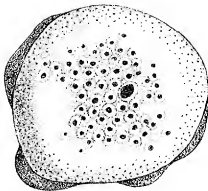




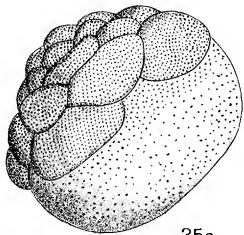
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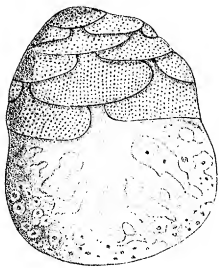
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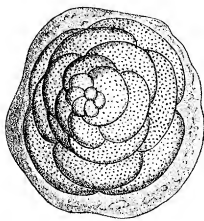
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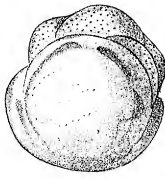
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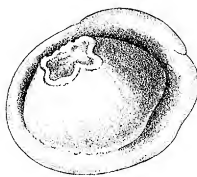
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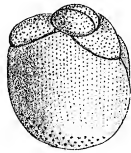
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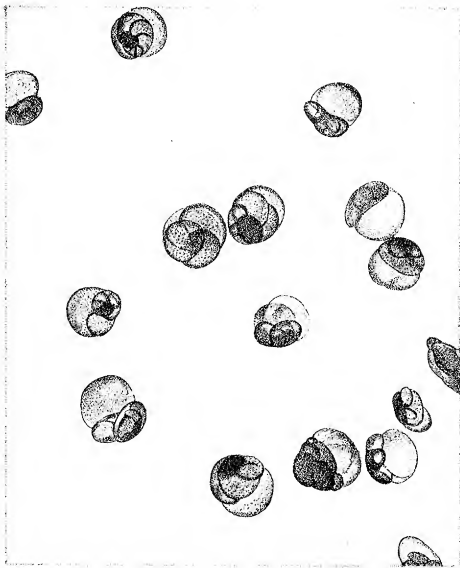
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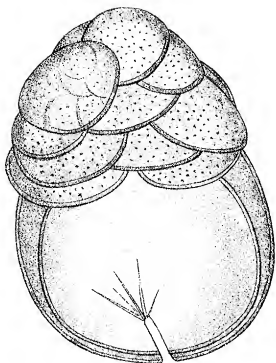
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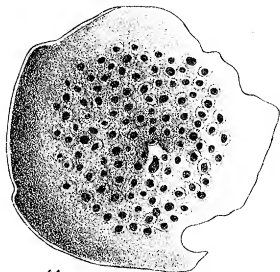
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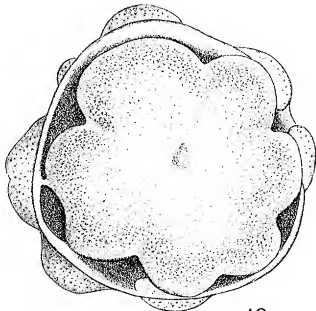
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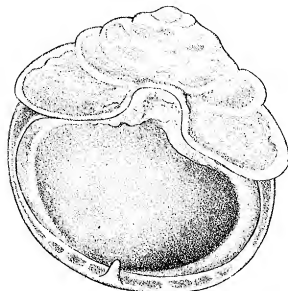
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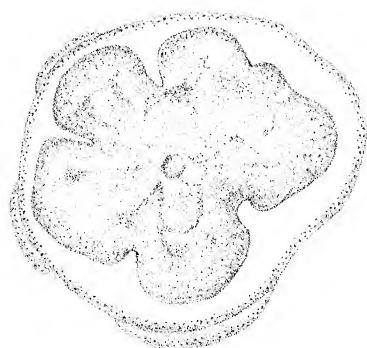
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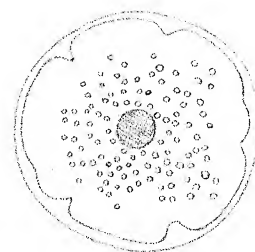
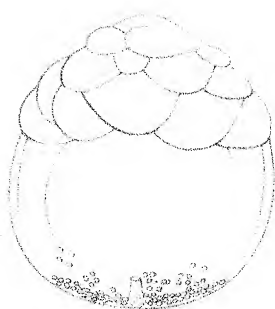
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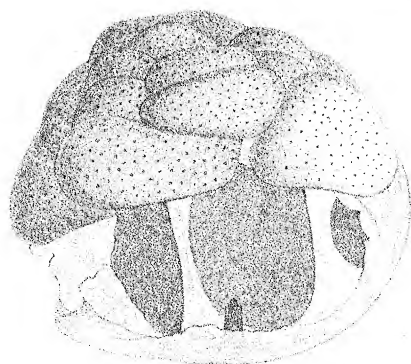
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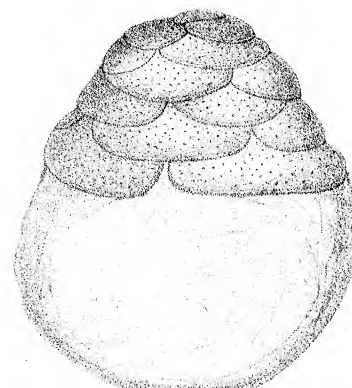
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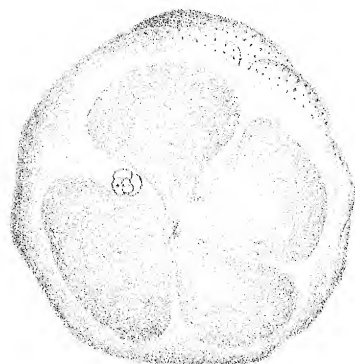
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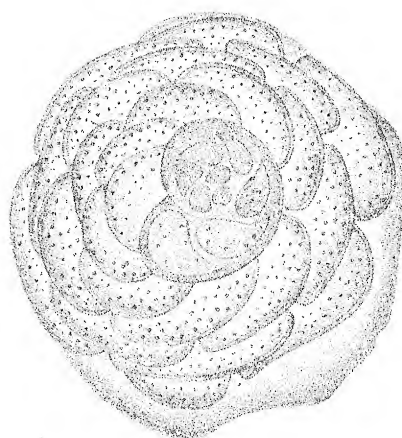
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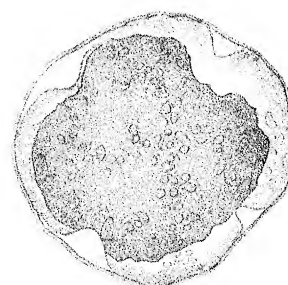
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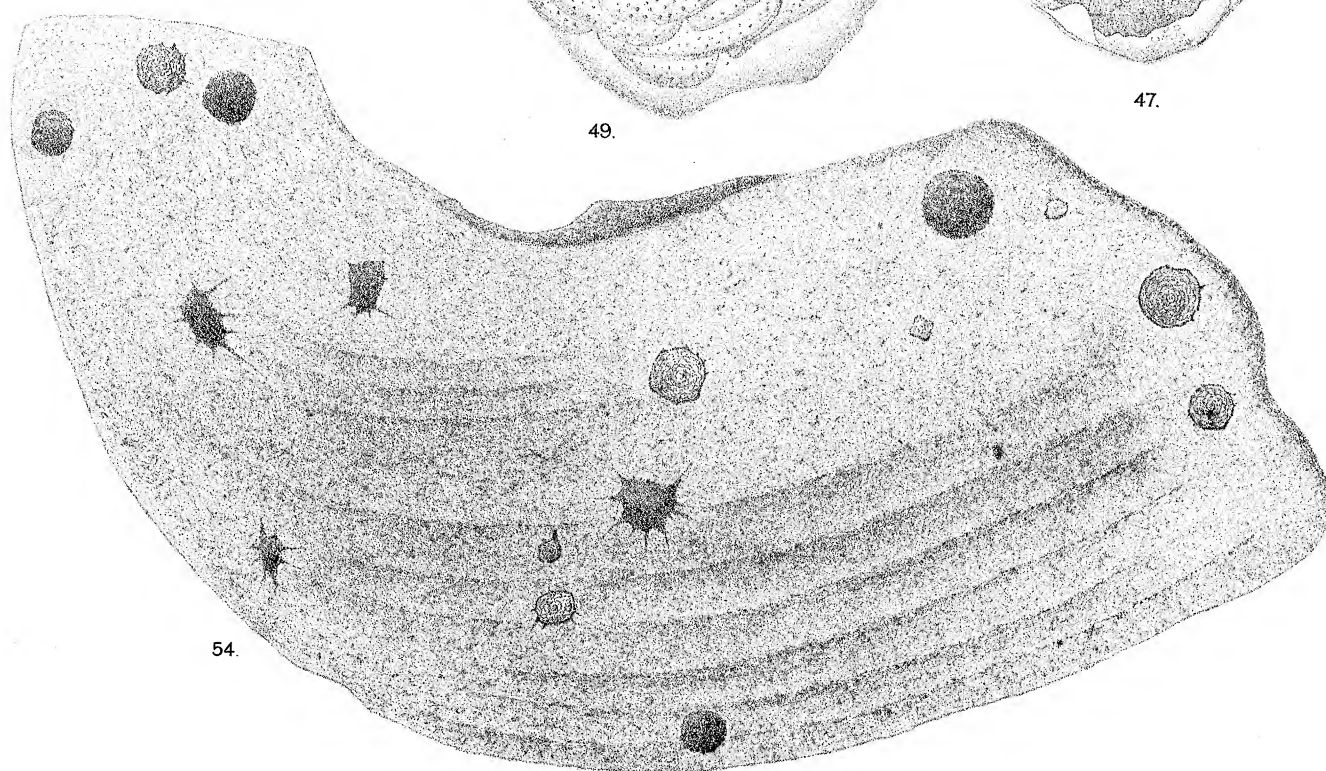
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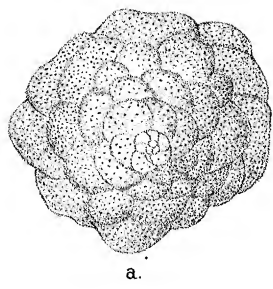
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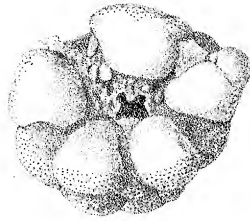
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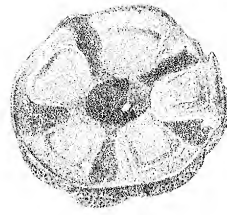
54.



a.



b.

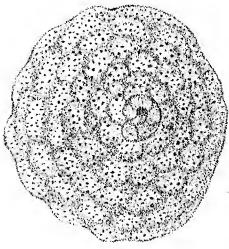


c.



d.

52.

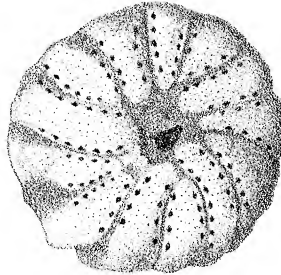


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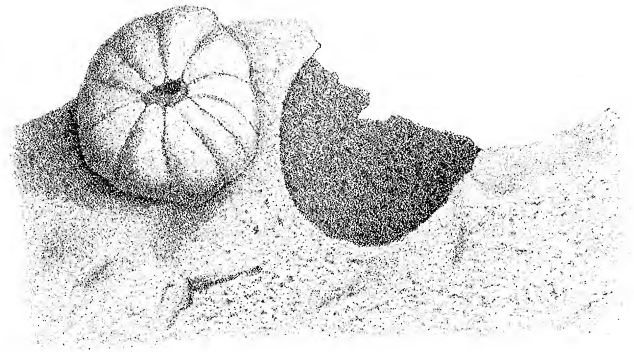


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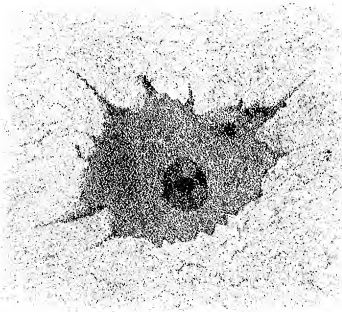
53.



b.



55.



56.



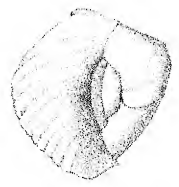
a.



b.



c.

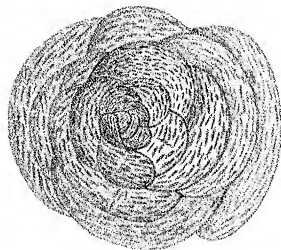


d.

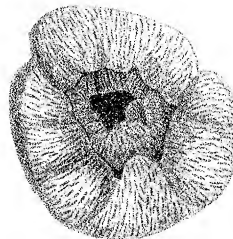
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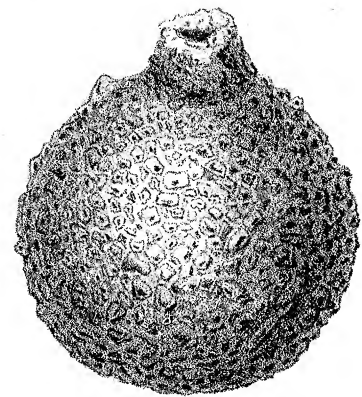
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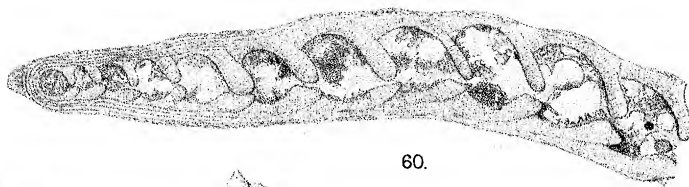
59a.



59b.



61.



60.



64.



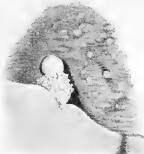
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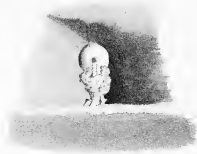
63.



65.



1.



2.



3.



4.

PLATE 13.

Fig. 1.—*Gromia dujardini* newly emerged from the mud on the floor of the aquarium.
(From Selsey Bill.) $\times 60$.

Fig. 2.—The same one hour later, climbing up the glass of the aquarium. $\times 60$.

Fig. 3.—The same an hour later, having climbed up the stems of alga. $\times 60$.

Fig. 4.—The same an hour later, having moved from the alga stems to the glass of the aquarium. $\times 60$.

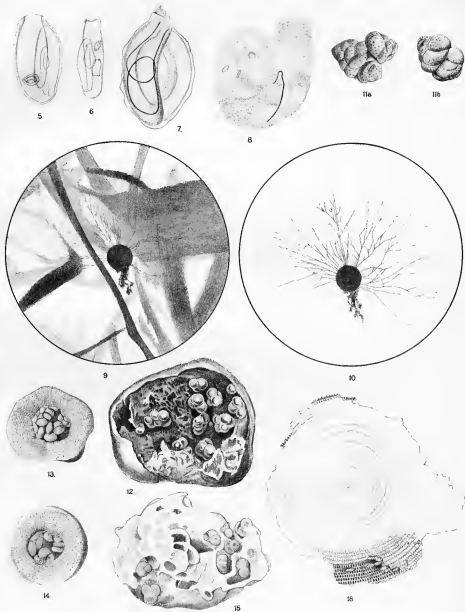


PLATE 14.

Fig. 5.—*Miliolina durrandii*, Millett, containing an embryonic *Massilina secans*. $\times 75$.

Fig. 6.—The same, a smaller specimen, containing two diatoms. (From the Kerimba Archipelago.) $\times 75$.

Fig. 7.—*Massilina secans*, viewed by transmitted light after having ingested a hair, or cloth filament. $\times 40$.

Fig. 8.—A similar specimen decalcified after ingestion of a hair. $\times 45$.

Fig. 9.—A lost specimen of *Gromia*, attracted into the circle of light formed by a hole punched in black paper and illuminated. Its first appearance. $\times 60$.

Fig. 10.—The same, after clearing away the weeds. $\times 60$.

Fig. 11.—(a) Triple and (b) double "association" of individuals of the species *Discorbina globosa*, Sidebottom. (From the Kerimba Archipelago.) $\times 130$.

Fig. 12.—*Discorbina mediterraneensis*, with contained young brood. (From Clare Island.) $\times 200$.

Fig. 13.—*Discorbina wrightii*, with contained young brood. (From Bognor.) $\times 130$.

Fig. 14.—*Discorbina parisiensis*, with contained young brood. (From West Scotland.) $\times 130$.

Fig. 15.—*Planorbudina mediterraneensis*, with contained young brood. (From Bregançon Bay, Hyères.) $\times 75$.

Fig. 16.—*Orbitolites complanata*, with young brood occupying the peripheral chambers. $\times 8$. From the Kerimba Archipelago.

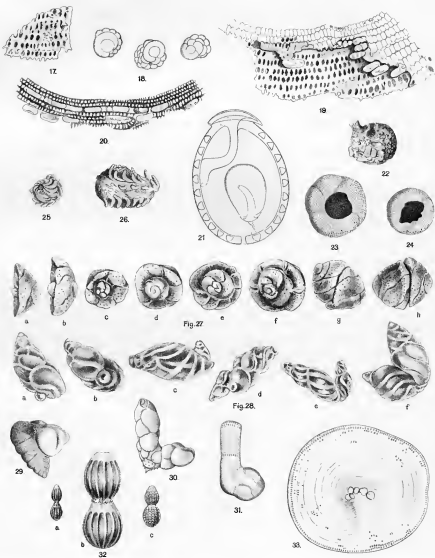


PLATE 15.

- Fig. 17.—The same, fragments of partially resorbed shell-wall removed. $\times 12$.
- Fig. 18.—The same, embryonic young removed. $\times 24$.
- Fig. 19.—The same, part of fig. 16 more highly magnified. (From the Kerimba Archipelago.) $\times 12$.
- Fig. 20.—*Orbitolites complanata* with viviparous young. Section of edge viewed by transmitted light. (From the Kerimba Archipelago.) $\times 12$.
- Fig. 21.—*Lagena ornata* (Williamson) containing fully developed young shell. $\times 320$.
- Fig. 22.—Young (Adelosine) stage of *Miliolina agglutinans* (d'Orb.) with sand grains. (From the Kerimba Archipelago.) $\times 60$.
- Figs. 23 and 24.—Empty shells of *Discorbina parisiensis* after the escape of the young shells. (From Bognor.) $\times 130$.
- Fig. 25.—Glauconitic cast of the protoplasmic bodies of an associated pair of *Discorbina pileolus* (d'Orbigny.) (From New Zealand.) Superior view. $\times 40$.
- Fig. 26.—The same—edge view. $\times 80$.
- Fig. 27.—*Discorbina parisiensis*, a-h, a series of "associated" pairs, the juvenile ranging from a single chamber to an adult shell. (From the Kerimba Archipelago.) $\times 100$.
- Fig. 28.—*Bulimina elegantissima*, a-f, a similar series. (From Dekos.) $\times 100$.
- Fig. 29.—*Textularia agglutinans*, monstrous specimen in which a second and deformed shell has proceeded from (?) damage of the original test. (From Loch Sunart, West Scotland.) $\times 25$.
- Fig. 30.—*Bulimina elegans*, a double specimen. (From Loch Sunart, W. Scotland.) $\times 65$.
- Fig. 31.—*Hauerina compressa* (d'Orbigny), a specimen in which a litiiform (Peneropline) chamber has been added to the adult shell. (From the Kerimba Archipelago.) $\times 40$.
- Fig. 32.—(a) *Lagena williamsoni* (Alcock), (b) *Lagena costata* (Williamson), (c) *Lagena squamosa* (Montagu), double specimens.
- Fig. 33.—*Orbitolites complanata*, specimen with five primordial chambers. (From the Kerimba Archipelago.) $\times 12$.

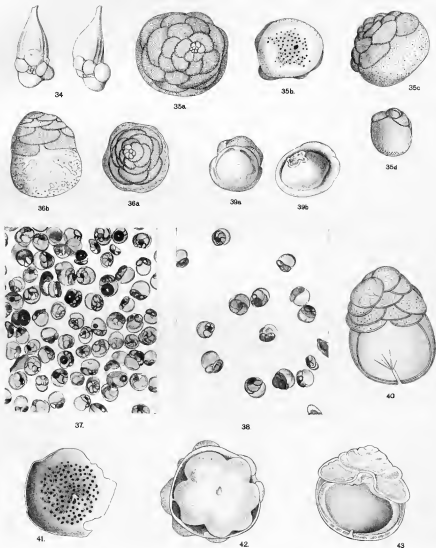


PLATE 16.

Fig. 34.—Monstrous or multiform Foraminifer, combining the rotaline and nodosarine plans of growth. (From Loch Sunart, W. Scotland.) $\times 95$.

Fig. 35.—*Cymbalopora bulloides* (d'Orbigny). (a) Superior view; (b) inferior view; (c) side view; (d) small variety. $\times 65$.

Fig. 36.—*Cymbalopora milletti*, Heron-Allen and Earland. (a) Superior view; (b) side view. (From the Kerimba Archipelago.) $\times 65$.

Fig. 37.—*Cymbalopora*, shore gathering, Corny Point, Yorke Peninsula, S. Australia (MATTHEWS, 1880). $\times 12$.

Fig. 38.—*Cymbalopora*, pelagic specimens taken in the tow net, Honolulu Harbour (MURRAY, 1875). $\times 12$.

Fig. 39.—*Cymbalopora bulloides* (d'Orbigny), with abnormal or immature balloon-chambers. $\times 95$.

Fig. 40.—*Cymbalopora bulloides* (d'Orbigny), the entosolenian tube, terminating in spines. $\times 130$.

Figs. 41 and 42.—*Cymbalopora bulloides*, the balloon-chamber removed; and the float-chamber thus exposed, showing contained desiccated organisms, ? *Xanthella*. $\times 65$.

Fig. 43.—*Cymbalopora bulloides*, section showing balloon and float and entosolenian tube. $\times 65$.

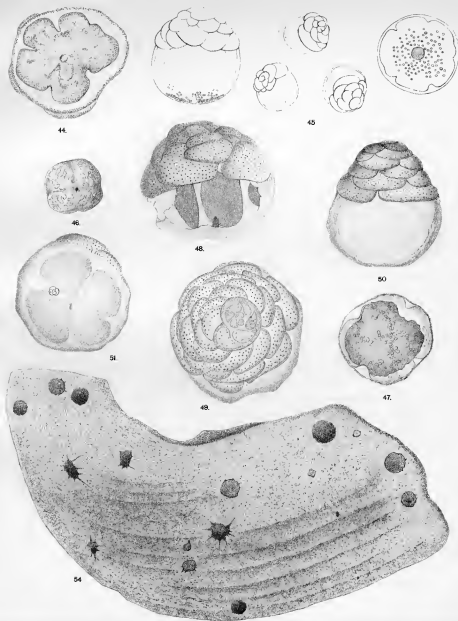


PLATE 17.

- Fig. 44.—*Cymbalopora bulloides*, with the float-chamber filled with ?*Xanthella*.
By transmitted light. $\times 65$.
- Fig. 45.—*Cymbalopora bulloides*, with the float-chamber indicated (after BRADY and MURRAY).
- Fig. 46.—*Cymbalopora milletti*, showing the constrictions of the balloon-chamber.
 $\times 95$.
- Fig. 47.—*Cymbalopora milletti*, after removal of the rotaline portion, showing the adherent walls of the "balloon" and "float," in three planes (diagrammatic): (i) broken terminal chamber; (ii) float-chamber adherent except at lobulations; (iii) the perforated base. $\times 130$.
- Fig. 48.—*Cymbalopora milletti*, showing the "struts" formed by the lobulations of the float-chamber (side of terminal chamber removed). $\times 150$.
- Fig. 49.—*Cymbalopora bulloides*, showing the rotaline aboral portion. $\times 130$.
- Fig. 50.—*Cymbalopora milletti*, showing the acervuline aboral portion. $\times 130$.
- Fig. 51.—*Cymbalopora milletti*, with (?) a rotaline embryo between the balloon- and float-chamber. $\times 130$ (slightly diagrammatic).
- Fig. 54.—*Cymbalopora tabelliformis*, Brady, a colony encrusted in a molluscan fragment (nine crypts empty). $\times 15$.

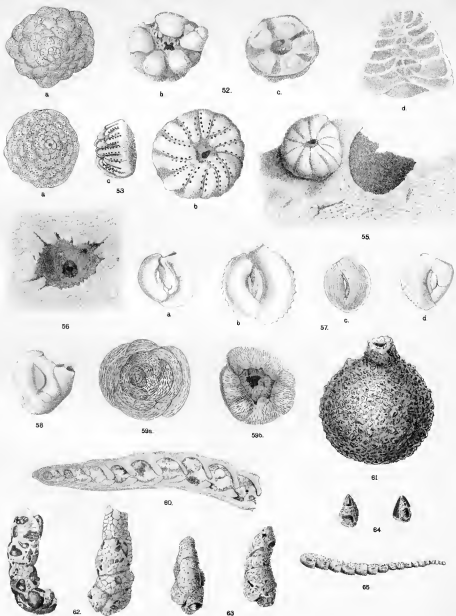


PLATE 18.

Fig. 52.—*Cymbalopora poeyi*, d'Orbigny: (a) superior view; (b and c) inferior view; (d) section of high-domed specimen. $\times 65$.

Fig. 53.—*Cymbalopora tabellaformis*, Brady: (a) superior view; (b) inferior view; (c) side view. $\times 50$.

Fig. 55.—*Cymbalopora tabellaformis*, a specimen removed and set beside its crypt. $\times 50$.

Fig. 56.—A crypt of *Cymbalopora tabellaformis* from fig. 54, showing the radiating passages. $\times 50$.

(Figs. 55–56 are from the Kerimba Archipelago and Sir JOHN MURRAY'S Collection.)

Fig. 57.—(a) *Massilina secans* (d'Orbigny); (b) var. *denticulata* (Costa); (c) var. *tenuistriata* (Earland); (d) var. *obliquistriata* (Halkyard). Grown in captivity at Selsey. $\times 25$.

Fig. 58.—*Massilina secans*, monstrous specimen, caused by damage in the aquarium repaired by the animal. $\times 25$.

(Figs. 57 and 58 from Selsey. Bred in tanks.)

Fig. 59.—*Carterina spiculotesta* (Carter): (a) superior view; (b) inferior view. (From Torres Straits.) $\times 100$.

Fig. 60.—*Vaginulina linearis* (Montagu). Section showing the deposition of layers of carbonate of lime outside the shell. (From the North Sea.) $\times 65$.

Fig. 61.—*Saccammina spherica* (M. Sars). (From the North Sea.) $\times 35$.

Figs. 62–64.—Arenaceous Foraminifera, showing the selection and incorporation of gem-fragments in the test.

Fig. 62.—*Haplophragmium agglutinans* (d'Orbigny). (From Selsey.) $\times 60$.

Fig. 63.—*Verneulina polystropha* (Reuss). (From Selsey.) $\times 40$.

Fig. 64.—*Reophax difflugiformis* (Brady). (From New Zealand.) $\times 40$.

Fig. 65.—*Reophax scottii* (Chaster). (From the North Sea.) $\times 55$.